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Dynamics in Saginaw Bay, Lake Huron

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MODELING OF PHYTOPLANKTON-NUTRIENT DYNAMICS IN SAGINAW BAY, LAKE HURON

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ABSTRACT. A multi-class, phytoplankton simulation model was developed and calibrated to an extensive set of field data acquired on Saginaw Bay, Lake Huron, during 1974. Phytoplankton biomass was partitioned into five functional groups: diatoms, greens, non- N_2 -fixing blue-greens, N_2 -fixing blue-greens, and "others." Nutrients included in the model were phosphorus, nitrogen, and silicon. The model was applied to a single spatial segment encompassing the inner portion of Saginaw Bay.

Process level analyses were conducted with the calibrated model to determine the relative importance of various factors affecting phytoplankton and nutrient dynamics. The concept of a single limiting factor for phytoplankton growth was found to be overly simplistic. Results indicated that temperature and light were relatively more growth rate limiting than nutrients on an annual average basis. However, as a consequence of nutrient depletion, nutrients became relatively more important at the times of peak phytoplankton crops. Nitrogen was found to be relatively more growth rate limiting than phosphorus to the total phytoplankton crop, although important differences occurred among the individual functional groups. At various times, and for various groups, all three nutrients were important in limiting either the rates of growth and/or the maximum sizes of the phytoplankton crops. Results were consistent with the hypothesis that while nitrogen and silicon were important in phytoplankton-nutrient dynamics, the supply of phosphorus would ultimately determine the size of the blue-green component of the total crop because N_2 -fixing blue-greens do not have absolute requirements for dissolved available nitrogen or silicon. Results indicated that phosphorus requirements of spring and fall diatom crops were satisfied primarily by external loadings. Phosphorus requirements of summer blue-green crops were satisfied primarily by recycle processes within the water column. Upon cell death, direct nutrient recycle to the available nutrient compartments in the water column from excess internal phytoplankton stores was found to be important for both phosphorus and nitrogen. Phytoplankton production was found to be extremely sensitive to variations in the light extinction coefficient in the water column, and relatively insensitive to variations in incident solar radiation.

INTRODUCTION

Saginaw Bay is a broad, shallow extension of the western shore of Lake Huron (Figure 1). The bay is oriented in a southwestward direction and is approximately 82 km long and 42 km wide. Saginaw Bay is usually divided into the indicated inner and outer portions. These portions are approximately equal in surface area; however, only 30 percent of the total water volume is contained in the inner portion because average depths of the

inner and outer portions are approximately 6 m and 15 m, respectively.

The total area of the Saginaw Bay watershed is approximately 21,000 km². The Saginaw River is the major tributary, accounting for over 90 percent of total tributary inflow to the bay. The principal land use categories in the watershed are agriculture and forest. The total population of the watershed is slightly over 1.2 million. Most of the population is concentrated into four major urban-industrial centers in the State of Michigan: Bay City, Midland, Saginaw, and Flint. These centers are all situated along the Saginaw River or its major tributaries.

The principal water uses in Saginaw Bay include

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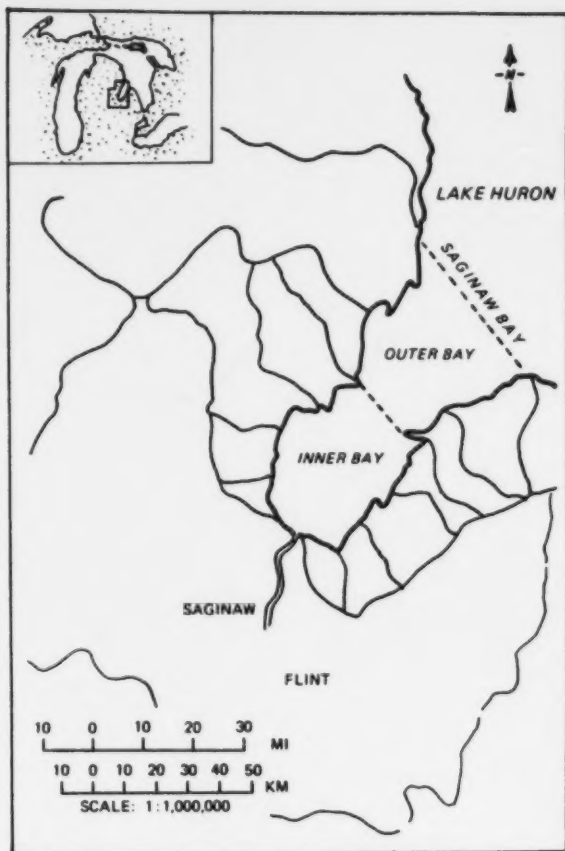


FIG. 1. Saginaw Bay and its watershed.

municipal and industrial water supply, waterborne transportation, recreation, commercial fishing, and waste assimilation. These uses are severely impacted by considerable quantities of waste discharges and runoff to the bay as a result of human activities in the watershed. Saginaw Bay has been identified by the International Joint Commission (IJC) as one of 44 Great Lakes "Problem Areas" (Great Lakes Water Quality Fifth Annual Report—Appendix B 1977).

Taste and odor and filter-clogging problems experienced by municipal water treatment plants on Saginaw Bay were especially important in motivating the present study. On the basis of daily measurements over an annual cycle at the Saginaw-Midland water supply system (Chartrand 1973), 42 percent of threshold odor values were found to be equal to or greater than the U.S. Public Health Service standard. Statistical analyses of these data revealed a strong correlation between threshold

odor number and phytoplankton cell number concentration, particularly for the blue-green component of the total crop. Bratzel, Thompson, and Bowden (1977) suggested that high threshold odor numbers appeared to be due to the products of decomposition of algal biomass by Actinomycetes (aquatic fungi), and by the blue-green algae themselves.

To address these and other water quality problems on Saginaw Bay, a research effort was initiated as part of the Upper Lakes Reference Study (ULRS) sponsored by the IJC. The goal of the ULRS was to acquire baseline data on water quality conditions in Lake Superior and Lake Huron. The effort on Saginaw Bay included the development of water quality models, in conjunction with comprehensive field and laboratory experimental studies.

The principal issue addressed in the development of the present model was cultural eutrophication, defined as overproduction of phytoplankton biomass due to increased nutrient loadings as a result of man's activities in the watershed. A deterministic phytoplankton simulation model was developed to describe the cause-effect connection between external nutrient loading and phytoplankton growth in Saginaw Bay, with particular regard to distinctions among the principal functional groups of phytoplankton. The objectives were twofold: first, to gain insight into the relevant physical, chemical, and biological processes affecting phytoplankton growth; and second, to use the model as a tool for comparing future effects of various wastewater management strategies.

SCOPE

The present model has been developed in the form of a spatially simplified version, and a spatially segmented version. The spatially simplified version was calibrated to a comprehensive set of field data acquired during 1974 on Saginaw Bay. Results from this version were used to develop the target phosphorus load to Saginaw Bay as part of the 1978 Water Quality Agreement between the U.S. and Canada (Vallentyne and Thomas 1978). Subsequently, after experience had been gained in applying the basic conceptual framework without the complications of spatial detail, the spatially segmented version was developed and calibrated to field data for 1974, as well as 1975. The more detailed results from the spatially segmented version will be compared to the outcome of a re-survey

conducted on the bay during 1980 to assess the response to a substantial phosphorus load reduction.

The present paper contains a brief description of the principal variables and processes included in the model, and a discussion of results from the spatially simplified version. This version is more convenient for use as a research tool to gain insight into the various biological and chemical processes. Calibration results are presented and summarized for the model state variables. Analyses of process level results are presented for phytoplankton growth rate limiting factors, phytoplankton loss rates, and nutrient recycle. Finally, results of sensitivity analyses conducted with the calibrated model are presented.

MODEL DEVELOPMENT

Rationale and Approach

A complete account of the rationale and approach used in development of the model is beyond the scope of this paper. This section contains a discussion of the mass balance approach used in developing the model equations, and summary

descriptions of the individual process mechanisms used. Appendices A-D contain the model equations and values for phytoplankton, zooplankton, and nutrient coefficients in the final calibration. A more complete treatment of model development is contained in Bierman *et al.* 1980.

Phytoplankton

Phytoplankton biomass, on the basis of dry weight, was resolved into five functional groups: diatoms, greens, N_2 -fixing (heterocystous) blue-greens, non- N_2 -fixing (non-heterocystous) blue-greens, and "others" (Figure 2). The last category included primarily dinoflagellates and cryptomonads. Heterocystous blue-greens consist of those species capable of fixing atmospheric nitrogen, as well as using dissolved combined nitrogen. Non-heterocystous blue-greens consist of those species which have an absolute requirement for dissolved combined nitrogen.

There are important physiological differences among the five functional groups of phytoplankton. Diatoms are the only group with a major absolute requirement for silicon. The N_2 -fixing blue-greens are the only group which can grow

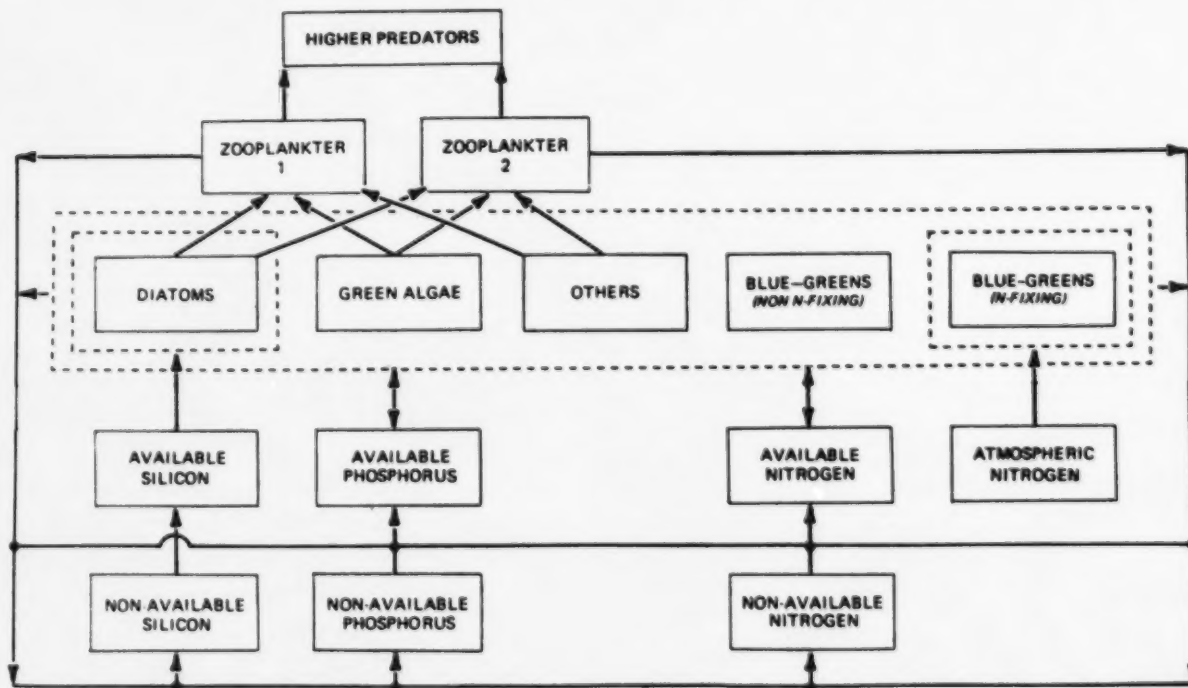


FIG. 2. Schematic diagram of principal model variables and interaction pathways.

independently of the supply of dissolved available nitrogen, defined as the sum of nitrogen in ammonia, nitrate, and nitrite. The relative maximum growth rates and temperature optima among the groups are such that a typical successional pattern during the growing season begins in spring with diatoms, progresses to greens and "others," and finally leads to the development of blue-greens in later summer and fall (Canale and Vogel 1974). An important characteristic shared by all of the groups is an absolute requirement for phosphorus.

Another important basis for differentiation was preferential grazing by zooplankton. Diatoms, greens, and "others" are generally considered to be acceptable food sources for zooplankton. Many species of blue-greens, including those frequently responsible for nuisance blooms, are not acceptable (Arnold 1971). McNaught *et al.* (1980) have hypothesized that the presence of sheaths around many bloom-forming blue-green species is an important factor in zooplankton food selection.

Nutrients

The nutrients included in the model were phosphorus, nitrogen, and silicon. These are generally considered to be the most important nutrients limiting growth rates and maximum sizes of phytoplankton populations in natural waters. On the basis of bioassay experiments with natural populations, Schelske, Rothman, and Simmons (1978) reported that phosphorus is the principal growth-limiting nutrient in all of the Great Lakes except Lake Erie. In Lake Erie, a higher relative supply of phosphorus leads to severe depletion of dissolved available nitrogen in the western basin. In Saginaw Bay, the importance of silicon is indicated by its severe depletion during the spring phytoplankton peak (Smith *et al.* 1977). Although carbon constitutes a larger proportion of phytoplankton biomass than either phosphorus or nitrogen, carbon was not included explicitly in the model. Considerable evidence that carbon is rarely growth-limiting to phytoplankton has been obtained in the *in situ* work by Schindler *et al.* (1973) and Schindler and Fee (1973) in Canadian Shield lakes, and in the laboratory experiments by Goldman, Oswald, and Jenkins (1974).

Space and Time Scales

The spatial and temporal scales used were largely dictated by the resolution of the field data available for comparison with model output. Other impor-

tant considerations were computational complexity and the stage of development of the model.

The present spatially simplified version of the model described only the inner portion of Saginaw Bay (Figure 1). This version can not describe any of the spatial gradients in water quality that exist in the inner bay. Smith *et al.* (1977) showed that there are horizontal gradients in this region, but that the inner bay is well-mixed in the vertical.

Field data were available for comparison with model output on approximately a monthly time scale. There were 13 sampling cruises on Saginaw Bay in 1974 during the period from late-March to mid-December. The time interval between each cruise varied from 18 days to one month. Neither the high frequency phenomena that occur over a 24-hour cycle, nor the sharp transient variations in water movements that occur due to the shallow nature of the inner bay were described by the model.

Mass Balance Kinetics

The principal variables, or state variables, in the model were expressed in the form of dynamic mass balance equations. Each equation corresponded to a mass balance for a single chemical or biological constituent. The state variable equations constituted a system of simultaneous, ordinary, nonlinear differential equations. The general form of these equations can be expressed in the following manner:

$$V_{\text{bay}} \frac{d C_{\text{bay}}}{dt} = Q_{\text{inflow}} C_{\text{boundary}} - Q_{\text{outflow}} C_{\text{bay}} + \text{sources} - \text{sinks}$$

- where C_{bay} = concentration of constituent in inner bay
 V_{bay} = volume of inner bay
 Q_{inflow} = net inflow from outer portion of bay to inner portion
 C_{boundary} = concentration of constituent at boundary between inner and outer portions of bay
 Q_{outflow} = net outflow from inner portion of bay to outer portion
 source = rate of change for a process which causes an increase in C_{bay}
 sink = rate of change for a process which causes a decrease in C_{bay}

The first two terms on the right hand side of the equation account for changes in mass due to water circulation effects. These effects could result in either positive or negative changes in mass balance. The net circulation pattern in Saginaw Bay is counterclockwise, with Lake Huron water flowing in along the northwestern shore, and out along the southeastern shore (Figure 3). For the spatial and temporal scales in the model, $Q_{inflow} \approx Q_{outflow}$ because tributary inflows were generally small compared to the Lake Huron flow-through. Consequently, the net boundary contribution for a given constituent depended primarily on the concentration gradient between the inner and outer portions of the bay.



FIG. 3. Dominant water circulation pattern in Saginaw Bay (from Danek and Saylor 1977).

Phytoplankton Kinetics

Nutrient Uptake and Cell Growth

The phytoplankton nutrient uptake and growth processes in the model were described using an internal nutrient pool sub-model for phosphorus and nitrogen (Verhoff and Sundaresan 1972, Verhoff *et al.* 1973, Bierman *et al.* 1973). The principal advantages of using an internal nutrient pool model are that more realistic descriptions can be obtained of non-steady-state conditions and nutrient recycle. Major disadvantages include in-

creased computational complexity and the need to specify additional model coefficients.

The internal nutrient pool sub-model used has been validated against phosphorus and nitrogen uptake data from five different species of phytoplankton (Kasprzyk, Dolan, and Bierman 1980). The principal features of this sub-model were:

1. Growth rates depended on internal nutrient levels and not on external nutrient levels.
2. Nutrient uptake rate was a function of both external and internal nutrient levels.
3. The active internal nutrient pool which participated in the nutrient uptake mechanism was proportional to the total internal nutrient level. This was a feedback mechanism which prevented the cell from absorbing arbitrarily large amounts of a nutrient and depleting the external environment.

One of the consequences of an internal nutrient pool model is that there does not exist a unique value for net specific uptake rate, given a value for extracellular nutrient concentration. Instead, there exists a family of values, each corresponding to a different level of internal nutrient. Negative values for net specific uptake rate can occur with such a model, and these correspond to nutrient leakage back to the extracellular medium which has been observed under certain conditions (Nalewajko and Lean 1978; Button, Dunker, and Morse 1973).

Phytoplankton-silicon kinetics in the model were described using a conventional Monod hyperbolic equation to relate specific growth rate directly to extracellular silicon concentration (Guillard, Kilham, and Jackson 1973; Kilham 1975). However, there has been evidence that an internal nutrient pool model might be a more appropriate description for phytoplankton-silicon kinetics (Conway, Harrison, and Davis 1976; Davis, Breitner, and Harrison 1978). In any case, the silicon kinetics used in the present model should be considered provisional, pending the results of further research.

To determine specific growth rates when more than one nutrient was at sub-optimal levels, a threshold hypothesis was used (Rhee 1978, Droop 1974). According to this hypothesis, specific growth rate is controlled by the single nutrient in shortest supply, relative to the phytoplankton requirements. Consequently, at any given time, there is a unique limiting nutrient for any given phytoplankton group. Depending on the circumstances, control can shift from one nutrient to another as a function of time.

Respiration

Phytoplankton respiration losses were described using a temperature-dependent, first-order decay term. Respiration was intended to describe population losses due to self-maintenance requirements, especially under non-optimal conditions. In laboratory systems under optimum conditions, such losses usually account for a negligible proportion of phytoplankton gross production; however, under natural conditions, such losses can be considerable because vertically-averaged gross production rates are usually much lower, and respiration occurs throughout the water column.

Decomposition

There has been experimental evidence that bacterially-mediated decomposition of phytoplankton under aerobic conditions is an important loss mechanism for viable phytoplankton cells in the water column. DePinto and Verhoff (1977) reported that the presence of heterotrophic bacteria populations greatly accelerated decomposition and subsequent nutrient recycle of *Chlorella* and *Selenastrum* cultures as compared to cultures which were kept bacteria-free. Gunnison and Alexander (1975) reported similar results for different species of phytoplankton, and they suggested that decomposition of the cell wall is a major determinant of algal resistance to microbial decomposition.

The model included a temperature-dependent, second-order phytoplankton decay mechanism to simulate the effects of microbial decomposition. A detailed discussion of the rationale for this approach, including comparative simulations, has been presented by DePinto, Bierman, and Verhoff (1976). In essence, the decomposition rate for a given phytoplankton group was assumed to be proportional to the product of the concentration of that group and the concentration of total phytoplankton. This approach was based on the assumption that total phytoplankton concentration was proportional to bacterial concentration. Such an approximation is reasonable because phytoplankton biomass serves as the principal carbon source for bacteria in the water column. This approach to describing phytoplankton decomposition has the important practical advantage of not requiring a separate set of equations for describing bacterial kinetics.

Sinking

Phytoplankton sinking losses were described by

assigning a constant sinking velocity, or "escape velocity," to each phytoplankton group in the model. This velocity was intended to correspond to the net flux of phytoplankton from the water column to the sediment.

The present approach was motivated primarily by lack of more rigorous alternatives. In order to describe sinking losses in rigorous terms, it would have been necessary to consider the hydrodynamics of the system, and the physiology of the phytoplankton. There did not exist a calibrated hydrodynamic model of Saginaw Bay which could describe vertical transport. In addition, although it is well-known that phytoplankton sinking rates depend on their physiological state (e.g., Titman and Kilham 1976, Smayda 1974), it is not clear how to quantify this relationship. In previous work (Bierman, unpublished results), variable sinking velocities were used as a function of internal phosphorus and nitrogen levels in the phytoplankton; however, the equations used were somewhat arbitrary, and the results were not significantly different than the present results.

Nutrient Kinetics

Total and Available Forms

Each of the nutrients in the model was assumed to exist in two different forms: an available form which could be used directly for phytoplankton growth, and an unavailable form which could not be used by phytoplankton. Available phosphorus in the model corresponded to dissolved orthophosphorus in the field data; available nitrogen corresponded to the sum of ammonia and nitrate/nitrite nitrogen; and available silicon corresponded to dissolved silicate silicon. In reality, each of the unavailable nutrients consisted of both a dissolved and a particulate fraction; however, no operational distinction was made between these fractions in the model.

A temperature-dependent, first-order mechanism was used to describe the transformations from unavailable to available nutrient forms in the water column. The unavailable nutrient forms were each assigned a sinking velocity because they each contained a particulate fraction. The sinking velocity for the unavailable nutrient forms was conceptually identical to the sinking velocity for the phytoplankton; i.e., it corresponded to a net flux from the water column to the sediments.

Nutrient Recycle

Nutrient recycle for phosphorus and nitrogen in the model consisted of two distinct components: a component associated with the minimum cell quota, or minimum stoichiometry, required by the phytoplankton, and a component associated with the internal nutrient level in excess of the minimum cell quota. When loss of phytoplankton biomass occurred in the model due to grazing, decomposition, and respiration, the nutrient component associated with the minimum cell quota of this biomass was recycled to the unavailable compartment in the water column, and the nutrient component associated with the excess internal level of this biomass was recycled directly to the available nutrient compartment in the water column. This is in agreement with evidence (e.g., Rhee 1973) that the latter component consists of available nutrient forms and loosely-bound compounds which rapidly convert to available nutrient forms.

Silicon recycle in the model was handled differently than phosphorus or nitrogen recycle because an internal nutrient pool sub-model was not used for silicon. When the above biomass losses occurred for diatoms, the entire silicon content of the cells was recycled only to the unavailable silicon compartment in the water column. As was the case for phosphorus and nitrogen, unavailable silicon was subsequently transformed to available silicon by a temperature-dependent, first-order mechanism.

Zooplankton Kinetics

Two zooplankton types were included in the model and they were assumed to graze on the diatom, green, and "other" phytoplankton groups. Blue-greens were not grazed. The zooplankton types were differentiated on the basis of their maximum feeding rates, or ingestion rates. Higher predators, such as carnivorous zooplankton and fish, were not included explicitly as state variables.

Zooplankton specific growth rate was a function of maximum ingestion rate, assimilation efficiency, temperature, and phytoplankton concentration. Mechanisms proposed by Scavia and Eadie (1976) were used to calculate effective phytoplankton half-saturation coefficients and estimates for minimum concentrations of individual phytoplankton groups necessary to stimulate feeding. The need for such mechanisms arises from the fact that most data for phytoplankton-zooplankton interactions are not of the type that can be used directly in models which include more than one predator-prey pair.

Zooplankton loss rate was described by a temperature-dependent, two-component decay mechanism. Such a mechanism was a substitute for explicitly including an additional trophic level above zooplankton. For both phytoplankton and zooplankton, a constant refuge concentration was specified. For the phytoplankton, this was a concentration below which no zooplankton grazing could occur. For the zooplankton, this was a concentration below which no second-order predation could occur.

DATA BASE

As part of the ULRS, intensive field surveys were conducted on Saginaw Bay during 1974 and 1975. These surveys were coordinated by the Large Lakes Research Station (LLRS) of the U.S. Environmental Protection Agency (USEPA). They involved close cooperation among several different institutions.

This paper contains only brief descriptions of contributions from the different institutions. Complete information is contained in the individual project reports.

Chemical Data

Cranbrook Institute of Science (CIS) was the lead organization for the sample collection effort, and for conducting water chemistry and chlorophyll analyses (Smith *et al.* 1977). Thirteen sampling cruises were conducted on a 59-station grid at multiple depths (Figure 4). Analyses were con-

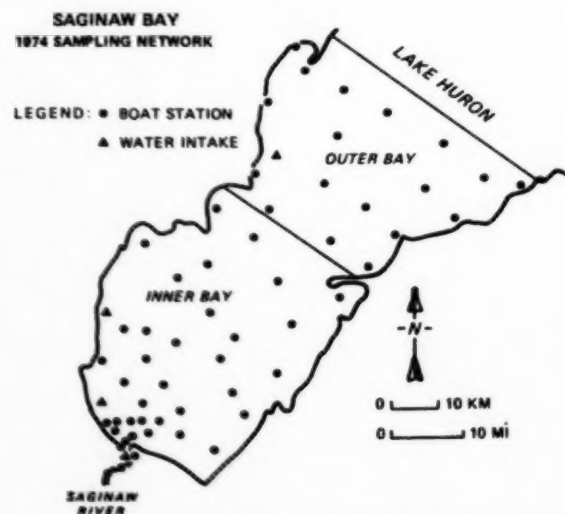


FIG. 4. Saginaw Bay sampling station network in 1974.

ducted for 22 different parameters, including phosphorus, nitrogen, silicon, chlorophyll, chloride, temperature, and Secchi depth. Average results for 33 stations in the inner portion of the bay were used for comparison with model output. Results for stations located in the Saginaw River, the principal tributary to Saginaw Bay, were used to calculate external nutrient loadings. Results for stations near the boundary between the inner and outer portions of the bay were used to specify boundary concentrations.

Phytoplankton Data

Phytoplankton samples were collected and analyzed by the Great Lakes Research Division (GLRD), University of Michigan (Stoermer *et al.*, in preparation). Samples were collected on the same cruises and at the same stations as the chemical samples. The only difference in the sampling design was that the phytoplankton samples were collected only at a depth of 1 meter. Analyses consisted of species identifications and cell number concentrations. Subsequently, an extensive series of cell volume measurements were conducted to transform the species count data to biomass values which were required for comparison with model output.

Zooplankton Data

Zooplankton samples were collected and analyzed by the University of Michigan Biological Station (UMBS), Pellston, Michigan (Gannon and Bricker, in preparation). The sampling design for zooplankton was identical to that for the chemical data, including multiple depths. As with the phytoplankton, analyses were conducted for species identifications and number concentrations. Measurements were later conducted for dry weights of the principal zooplankton species to provide data for comparison with model output.

External Loadings

Determination of external loadings is one of the most important factors in the application of a mathematical model. In the case of Saginaw Bay, these loadings originated from three different sources: tributary inputs, atmospheric deposition, and inflow of water from Lake Huron across the boundary between the inner and outer portion of the bay. By far the largest of these sources was tributary inputs, principally from the Saginaw River. The Saginaw River contributes approxi-

mately 95 percent of the total tributary loading to Saginaw Bay.

Nutrient loadings from the Saginaw River were determined on the basis of an intensive field sampling program. For the first half of the year, samples were collected at 2- to 3-day intervals at the Dow Chemical Company water intake plant at the mouth of the Saginaw River (Figure 4). From July to December, samples were taken from the Midland Street bridge in Bay City every 2 weeks. During the latter period, the Dow intake was strongly influenced by intrusion of water from the bay because of low-flow conditions in the river. The Midland Street bridge is approximately 8 km upstream from the river mouth and is not subject to intrusion. Chloride, total and dissolved forms of phosphorus and nitrogen, and dissolved silicon were measured. These data were augmented with similar measurements by the Michigan Department of Natural Resources (MDNR) on samples collected from the Midland Street bridge every 2 weeks.

Daily average flow rates were obtained from the U.S. Geological Survey (USGS) for the four major tributaries to the Saginaw River: the Cass, the Flint, the Tittabawassee, and the Shiawassee. A daily average flow for the Saginaw River was obtained by summing these four rates, along with a correction factor for the ungauged area near the mouth of the river.

Saginaw River loading rates were determined by calculating the product of flow and concentration for each constituent, and then identifying all significant peaks and troughs. Subsequently, annual time-series were formed for each constituent by linear interpolation between these significant values. As an example, Figure 5 contains the time-series used for total and available forms of phosphorus. Integration of the time-series for each constituent resulted in the total annual river load (Table 1). Results indicated a sharp seasonal dependence in the tributary loading for each constituent. Approximately 70 percent of the annual loading occurred in the first half of the year. This is a typical pattern in temperate zone lakes due to snowmelt and heavy spring runoff.

Atmospheric contribution to the total Saginaw Bay load was based on data from collection stations on Lake Huron that were established as part of the ULRS (Mullin 1976). Results indicated that the atmospheric load for total phosphorus was approximately 4 percent of the total phosphorus load from tributary sources.

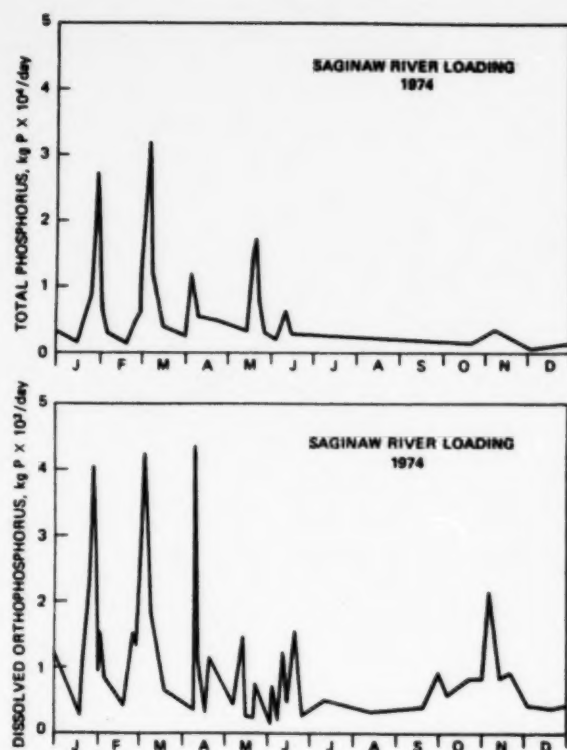


FIG. 5. Time series for Saginaw River loads for total phosphorus and dissolved ortho-phosphorus.

TABLE 1. Summary of Saginaw River loads for 1974.

Chemical Constituent	Total annual load in metric tonnes ¹
Total P	1,265
Dissolved PO ₄ -P	282
Total N	14,110 ²
Total Kjeldahl N	5,240
Dissolved NO ₃ -N plus NO ₂ -N	8,870
Dissolved NH ₃ -N	934
Dissolved SiO ₂ -Si	11,550
Chloride	325,600

¹Saginaw River constitutes approximately 95% of the total tributary load to Saginaw Bay. In addition, atmospheric phosphorus loading contributes 4% of the total phosphorus loading. Atmospheric loads for nitrogen and silicon have not been determined.

²Sum of annual values for TKN, NO₃-N, and NO₂-N.

Under certain conditions, boundary exchange constituted a net external loading for dissolved available nitrogen and silicon. During periods of severe nitrogen depletion in later summer, bound-

ary exchange constituted a temporary source for dissolved available nitrogen. During most of the year, boundary exchange constituted a sink for dissolved available silicon; however, for approximately 2 months after severe silicon depletion due to the spring diatom peak, boundary exchange constituted a net source. Boundary exchange for total phosphorus and total nitrogen constituted a nutrient sink for the inner bay because concentrations of these constituents were always lower in the outer bay.

MODEL CALIBRATION

Methods

Specification of external forcing functions and internal model coefficients are generally considered to be part of the model calibration process. Forcing functions include water temperature, incident solar radiation, external loadings, boundary conditions, and water exchange rates. These quantities were not calculated internally by the model; instead, they were determined independently and then supplied as input to the model. All forcing functions were specified to the model on a daily basis using linear interpolation between measured values.

Specification of internal model coefficients and comparison of resulting model calculations with field data is partly a science and partly an art. If all of the equations in the model were developed strictly from first principles, then it would be possible to uniquely determine all of the coefficients. In practice, the scientific literature is used as a basis for determining ranges and boundaries for model coefficients. The modeler then varies these coefficients within their reported ranges to obtain the best correspondence between model calculations and actual data. This is not strictly a curve-fitting process because coefficients are not allowed to assume arbitrary values to obtain the best fit in a strictly mathematical sense. If the model equations correspond well to the most significant dynamic processes which occur in the system, then the calibrated model will be physically realistic.

A dynamic mass balance model for chloride, a conservative tracer, was used to quantify water exchange rates for the inner bay. Figure 6 illustrates the external chloride loads, the comparison between model output and field data, and results for net water exchange rates between the inner and outer bay. These net exchange flows were used as input to the phytoplankton model in a piecewise

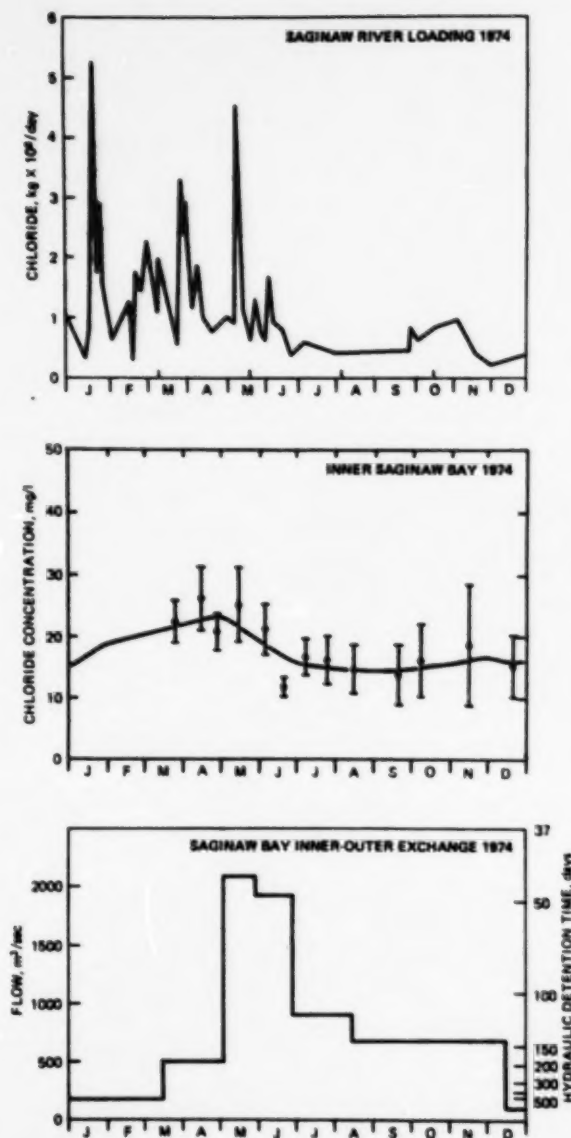


FIG. 6. External loadings, model calibration output, and results for net water exchange rates from the application of the conservative tracer model.

linear fashion. The average hydraulic detention time of the inner bay was found to be approximately 4 months. Water circulation was a highly dynamic process characterized by a slow, stagnant period early in the year, followed by a period of very rapid flushing during May-June. Subsequently, a stable summer-fall circulation was established.

Incident solar radiation was specified using monthly average values from Thomann *et al.* (1975) for Lake Ontario. Saginaw Bay and Lake Ontario lie at the same latitude. Lake Ontario values were modified to account for an ice cover which existed on the inner bay for the first 75 days in 1974.

Light extinction in the water column was specified using cruise average values for Secchi depth. Extinction coefficient values were calculated using a regression equation against inverse Secchi depth as an independent variable. The regression equation was developed using data from quantum measurements at various depths, and measurements of Secchi depth at each of 16 stations on 12 sampling cruises on Saginaw Bay during 1976. A statistically significant correlation at the 95% confidence level was found between extinction coefficient and inverse Secchi depth. Water temperature was specified using cruise average values from the sampling stations.

The model equations were solved numerically using an Adams-Moulton predictor-corrector algorithm. The time steps used were 30 minutes for internal and external dissolved nutrient concentrations, and 3 hours for all other equations. A typical 365-day run required approximately 15 minutes of CPU time on a Digital Equipment Corporation PDP-11/45 computer.

Geometric statistics were used to reduce the phytoplankton data and zooplankton data. Dolan *et al.* (1978) found that the phytoplankton data were log-normally distributed. Since the zooplankton data were based on species counts in a manner similar to the phytoplankton data, it was decided to use geometric statistics for these data as well. Conventional arithmetic statistics were used for all other parameters because they were based on direct concentration measurements, and were not found to be log-normally distributed.

All phytoplankton and zooplankton data are presented as the geometric mean plus or minus one standard deviation of the data points about the mean. All other data are presented as the arithmetic mean plus or minus one half standard deviation of the data points about the mean. The arithmetic deviations are presented differently because the data show large variations about the means, and it was decided to tighten the calibration criteria about the mean values. These large variations were due primarily to the spatial aggregation of dissimilar water masses into a single spatial segment.

The operational criterion for a successful calibration was to obtain model output as close as possible

to the mean value for each cruise, for each parameter. In cases where it was not possible to obtain model output within a standard deviation or half a standard deviation of the mean, an attempt was made to fit the peak concentrations as closely as possible, thus compromising the fit during off-peak periods. This resulted in the smallest relative error during periods when a given variable was most important.

Results

Biological Variables

Results for phytoplankton and zooplankton biomass concentrations are shown in Figure 7. In general, model output was within a standard deviation of the field data for most of the cruises, for each variable. Total phytoplankton crop ranged over greater than an order of magnitude. Diatoms accounted for approximately 99 percent of the total biomass in the spring peak. Total blue-green biomass accounted for approximately 70 percent of the total biomass in late summer and early fall. Greens and "others" accounted for relatively small fractions of the total phytoplankton crop. Table 2 contains summaries of peak phytoplankton concentrations and annual integrated gross production values for the individual phytoplankton groups in the calibrated model. An interesting observation was that, although peak total blue-green concentration was only 30 percent of peak diatom concentration, annual integrated gross blue-green production was 65 percent of annual integrated gross diatom production. These differences reflected the fact that the blue-green peak was much broader than the diatom peak.

From differences in the relative magnitudes of the two blue-green phytoplankton groups, it can be inferred that no significant degree of nitrogen fixation occurred in Saginaw Bay. This conclusion can not be confirmed because measurements of nitrogen fixation were not conducted.

The principal operational differences among the phytoplankton groups in the model that were responsible for the differences in concentrations and temporal behavior in the calibration results are summarized in Table 3. Some of these operational differences were built into the conceptual framework of the model, for example, the differences involving absolute nutrient requirements and zooplankton grazing. The differences involving maximum growth rates, temperature dependence

of growth rates, and phosphorus uptake efficiencies were not inherent to the conceptual framework of the model. These differences were imposed in the form of particular choices for various model coefficients on the basis of information from the literature, and/or by observations on the Saginaw Bay system.

Nutrient Variables

Results for total phosphorus and nitrogen concentrations are shown in Figure 8. Model output closely followed trends in the field data; however, agreement was not usually obtained to within one half a standard deviation. For both nutrients there were large increases early in the year, and sharp declines in the middle of the year. This pattern was a consequence of the time dependence of the external loadings and the water exchange rates.

Results for dissolved available forms of phosphorus, nitrogen, and silicon are shown in Figure 9. For phosphorus, model output was within half a standard deviation of the field data for most sampling cruises. For nitrogen and silicon, model output closely followed the trends of the field data; however, agreement was not usually obtained to within one half a standard deviation. The dissolved available nutrient concentrations were influenced substantially by the same principal factors as the total nutrient concentrations. Consequently, the trends observed for available concentrations, at least for phosphorus and nitrogen, were somewhat similar to the trends for total phosphorus and nitrogen. The principal additional factor affecting dissolved available nutrients was phytoplankton uptake. In addition, dissolved available silicon behaved differently because, after depletion due to the spring diatom peak, inflow from Lake Huron caused a sharp increase in the inner bay concentration.

DISCUSSION

A calibrated simulation model can be used as a tool to gain insight into the dynamics of a system. One approach is to analyze output from the calibrated model at the process level to determine the relative importance of different processes. Results of such analyses are presented here for various processes affecting phytoplankton and nutrient dynamics.

Results of the present analyses are only as valid as the assumptions used in constructing the model,

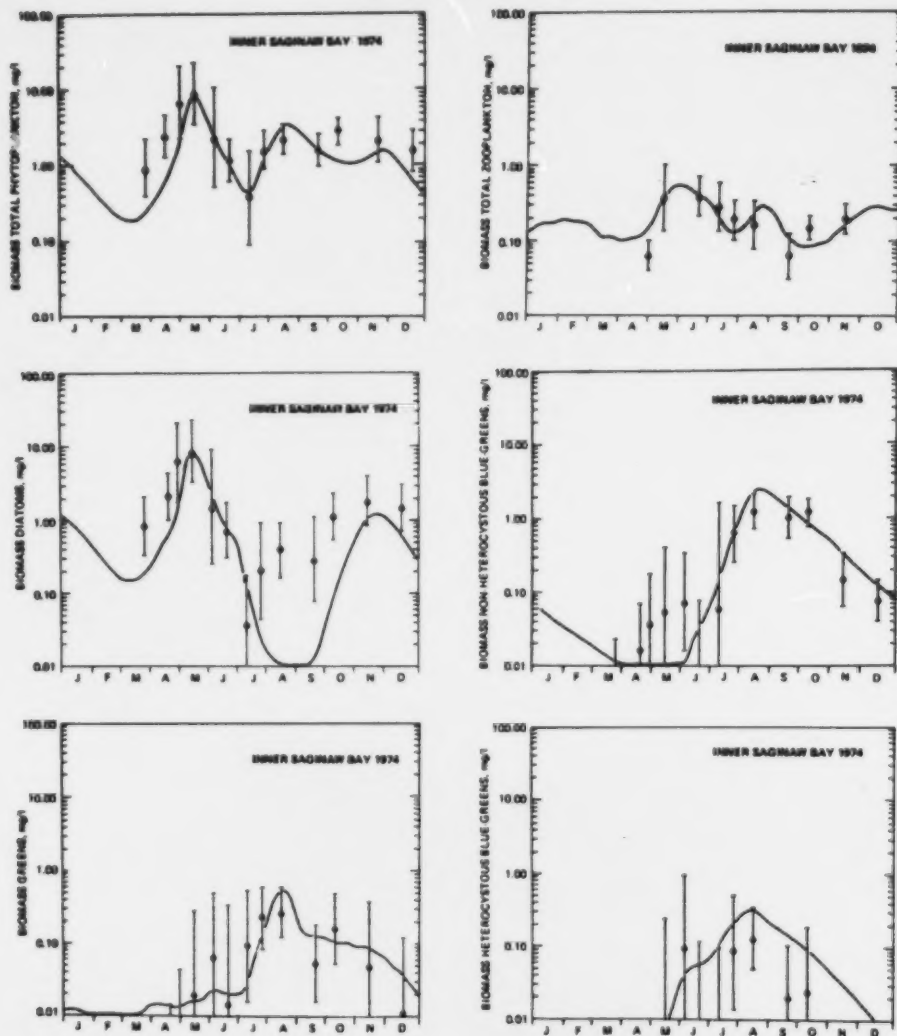


FIG. 7. Comparisons between model output and field data for phytoplankton and zooplankton biomass concentrations.

TABLE 2. Comparison among phytoplankton functional groups in model calibration results.

Phytoplankton Group	Peak Concentration mg/liter	Annual Integrated Gross Production ¹ mg/liter
Diatoms		24.8
spring peak	9.37	
fall peak	1.24	
Greens	0.57	3.5
Others	0.33	2.3
Blue-Greens (non-N ₂ -fixing)	2.56	14.0
Blue-Greens (N ₂ -fixing)	0.31	2.0

¹Time integral of daily gross biomass production over the annual cycle.

and the goodness-of-fit obtained in the calibration. There is no way to absolutely confirm that conclusions drawn at the process level are correct. Mathematical modeling results and experimental results should be used in a complementary fashion; however, neither approach by itself can provide a complete understanding of process dynamics. Mathematical models can provide information on individual processes over broad spatial and temporal scales within a mass balance framework. *In situ* experimental measurements can provide confirmatory information for many of these processes; however, it is usually impractical to conduct such

TABLE 3. Principal differences among phytoplankton groups in the model.

Characteristic Property	Diatoms	Greens	Others	Non-N ₂ -fixing Blue-greens	N ₂ -fixing Blue-greens
Absolute nutrient requirements	phosphorus nitrogen silicon	phosphorus nitrogen	phosphorus nitrogen	phosphorus nitrogen	phosphorus
Maximum growth rates under optimal conditions	high	moderately high	moderately low	moderately low	low
Phosphorus uptake efficiency	moderate	moderately high	moderate	high	moderate
Grazing by zooplankton	grazed	grazed	grazed	not grazed	not grazed

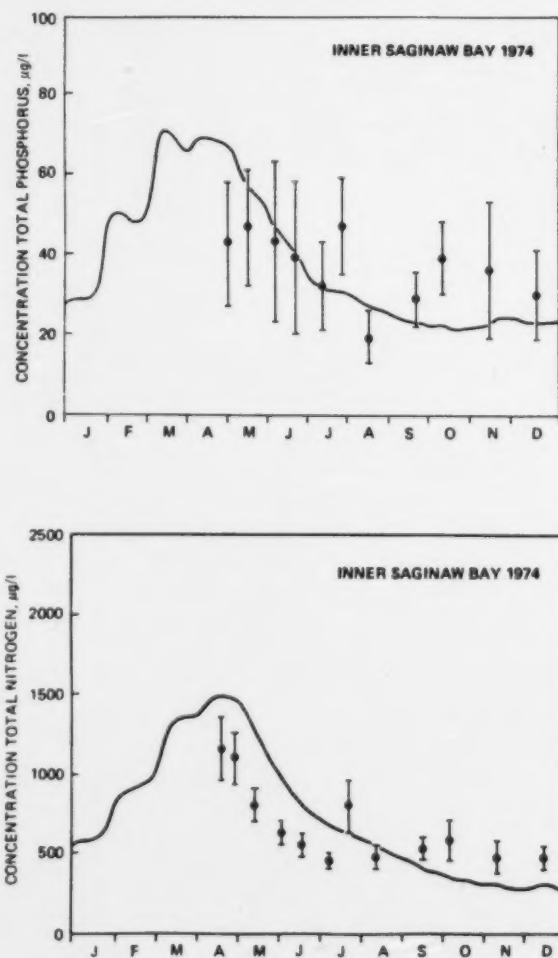


FIG. 8. Comparisons between model output and field data for total phosphorus and total nitrogen concentrations.

measurements over broad spatial and temporal scales. Consequently, it is rarely possible to completely validate a model at the process level, as well as at the state variable level.

Temperature and Light Limitation

The differences between maximum phytoplankton growth rates and actual specific growth rates that occur in the natural environment are a function of ambient temperature, light, and nutrient conditions. In general, these actual growth rates are much less than maximum growth rates observed in the laboratory. Although phytoplankton have absolute requirements for various nutrients, temperature and light effects are usually more limiting than generally realized.

Figure 10 contains typical results of process analyses of growth rate terms in the model equations using output for diatoms and non-N₂-fixing blue-greens. The curves in each figure represent progressive reductions from the maximum growth rate for each phytoplankton group. The indicated resultant growth rates correspond to vertically-averaged gross production rates.

Water temperature places an upper limit on the actual growth rate that can occur at any given time, independent of light and nutrient conditions. For each phytoplankton group, maximum growth rate can only occur during limited periods of the year. A bimodal pattern occurred for diatoms, partly because their specific growth rate as a function of temperature was assumed to reach a plateau at 10°C, and to decline after 14°C. Lin and Schelske (1978) reported the existence of such plateaus in specific growth rates for several Great Lakes diatoms. Stoermer and Ladewski (1976) reported that natural populations of *Stephanodiscus binderanus* and *Stephanodiscus tenuis* prefer tem-

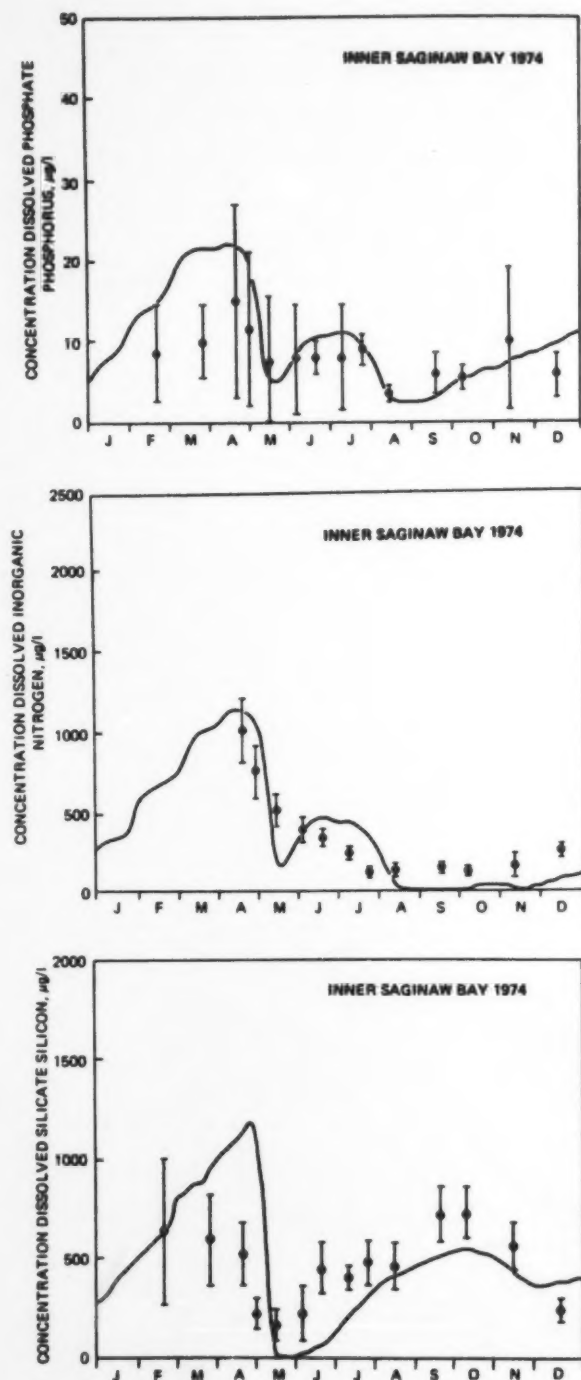


FIG. 9. Comparison between model output and field data for dissolved available concentrations of phosphorus, nitrogen, and silicon.

temperatures in the range from 6–9°C, and then rapidly decline after approximately 14°C. These two species accounted for most of the diatom biomass in inner Saginaw Bay. The pattern for non-N₂-fixing blue-greens was unimodal and coincided with higher temperatures. The growth rate for this group was assumed to be optimal at higher temperatures, and to decline at lower temperatures.

Substantial reductions in growth rates occurred due to light limitation. This was because gross production rates in the model were vertically averaged, and thus included the effect of exponential light extinction in the water column. Mortimer (1969) pointed out that actual growth rates are a function of the ratio of illuminated depth to stirred depth. For the values of incident solar radiation and water column extinction coefficients in this study, the illuminated depth was approximately 1.4 meters. That is, only the upper 1.4 meters of the water column contained saturation light intensities for phytoplankton growth. Since the average depth of the inner bay was 5.8 meters, 5.8 meters was also the stirred depth. Consequently, only 24 percent of the water column contained light intensities that were saturating for phytoplankton growth. In the remainder of the water column, light intensities were below saturating levels.

After nutrient reduction effects were taken into account, resultant mass growth rates in the model were found to average approximately 0.05–0.10 day⁻¹ over the annual cycle, with peak values of approximately 0.2–0.3 day⁻¹. These average values were consistent with experimental measurements conducted by Schelske *et al.* (1978) in various regions of the Great Lakes with natural assemblages. Peak values corresponded to mass doubling times of two to four days, and were consistent with experimental measurements by R. Moll (personal communication, Univ. of Michigan, Great Lakes Research Division) in the Saginaw Bay–Lake Huron system.

Phytoplankton Loss Processes

Phytoplankton net growth rate was equal to gross production rate minus the sum of rates for individual loss processes. These loss processes included respiration, sinking, grazing, and decomposition. Boundary flow could represent either a gain or a loss, depending on the direction of the concentration gradient.

Figure 11 contains typical results for the relative contribution of each loss process using output for

diatoms and non- N_2 -fixing blue-greens. The proportional contribution of a given loss process was calculated at each point in time by taking the ratio of that process rate to the sum of absolute values of all individual process rates. The sum of absolute values of the proportional contributions was equal to unity. All of the processes except boundary flow constituted net losses relative to gross production, and were assigned negative values. Boundary flow could constitute either a gain or a loss and was assigned either a positive or a negative value, respectively.

During periods of increasing phytoplankton concentration, boundary flow constituted a net loss for both phytoplankton groups. Phytoplankton concentrations during these periods were higher in the inner bay than in the inflow across the boundary between the inner and outer portions of the bay. This implied that peak phytoplankton crops observed in the inner bay were actually produced there, and were not due to water movements. During periods of low and/or decreasing phyto-

plankton concentrations, boundary flow constituted a positive contribution. This reflected the fact that there were differences in timing of the phytoplankton crops between the inner and outer portions of the bay. During periods when boundary flow contributions were positive, the sums of other loss terms usually exceeded those of boundary flows and, hence, boundary flow was never sufficiently large to cause a net increase in inner bay phytoplankton concentration.

Non-predatory death rates, expressed as respiration and decomposition, were quite significant, especially for blue-green algae. The importance of including such non-predatory death mechanisms as cellular breakdown and decomposition, and cell death through parasitism in mathematical models was emphasized by Jassby and Goldman (1974). It is interesting to note that more than 30 years ago, Riley (1946) recognized the importance of phytoplankton respiration. He suggested that as temperature increases, respiration can become a dominant population loss mechanism. Respiration in the

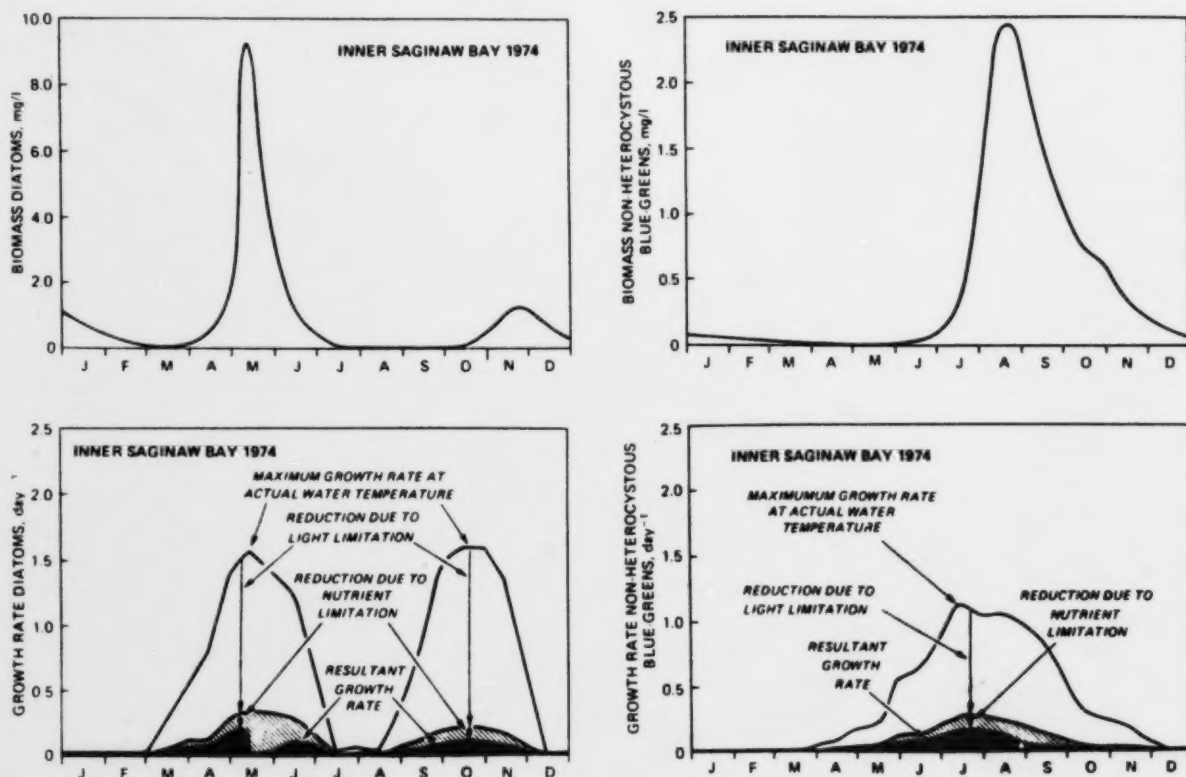


FIG. 10. Results of process level analyses for growth rates of diatoms and non- N_2 -fixing blue-greens.

model accounted for 15 to 50 percent of population losses for diatoms and greens, and for 20 to 65 percent of population losses for blue-greens. Decomposition accounted for approximately 25 percent of population losses for diatoms and greens, and for 40 percent of population losses for blue-greens during periods of peak total biomass.

During most of the year, sinking was the least important of the loss processes for all of the phytoplankton groups in the model. Part of the reason was that the net sinking rates used were relatively small because of the substantial vertical dispersion in the inner bay due to wind mixing and shallow depth. Sinking rate accounted for a larger proportion of total population losses during colder periods. This was because all other loss processes except boundary flow were temperature-dependent, whereas sinking rate was assumed to remain constant.

Grazing was the most significant loss process for diatoms and green algae during the July–August period. Grazing accounted for 25 to 70 percent of population losses for diatoms, and for 40 to 70

percent of population losses for green algae during this period. A detailed examination of model results indicated that from 3 to 90 percent of daily gross diatom production was grazed during April and May, and from 99 to 1,850 percent of daily gross diatom production was grazed during the July–August period. Corresponding results for green algae were 9 to 70 percent, and 24 to 130 percent of gross daily production grazed. These ranges were consistent with experimental measurements of grazing by zooplankton on natural phytoplankton populations in southern Lake Huron by McNaught *et al.* (1980). These results implied that phytoplankton in Saginaw Bay did not come under control by grazing until mid-summer.

Nutrient Limitation

The relative importance of phosphorus and nitrogen as limiting nutrients in the model was determined by comparing values for the internal levels of these nutrients in the phytoplankton to minimum stoichiometric requirements, or cell quotas. The

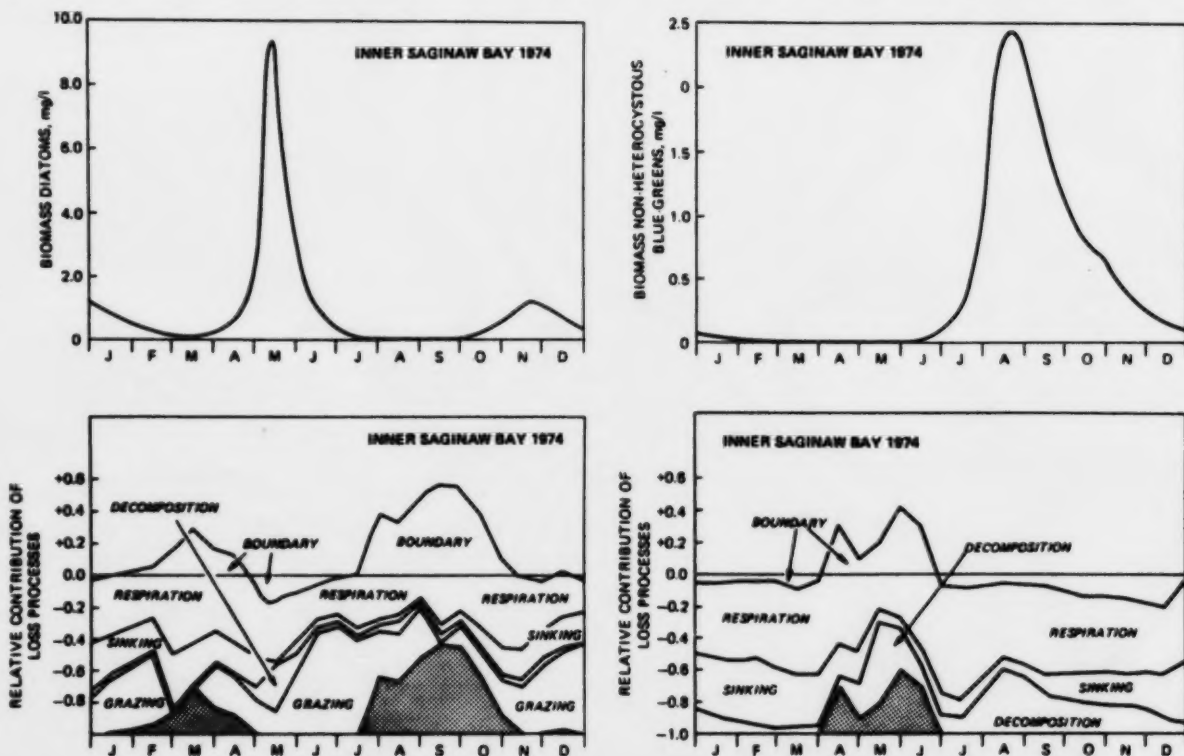


FIG. 11. Results of process level analyses for total loss rates of diatoms and non- N_2 -fixing blue-greens.

quantities appearing in the top graph of Figure 12 correspond to averages of the indicated ratios for all five phytoplankton groups. Results showed that nitrogen was consistently more rate limiting than phosphorus over the entire annual cycle. Only during May and August did internal phosphorus levels approach internal nitrogen levels. At all other times there was phosphorus sufficiency because internal phosphorus levels ranged from three to five times the minimum cell quotas.

The lower graph in Figure 12 illustrates the results of an independent check on the condition of phosphorus sufficiency in Saginaw Bay. The average of ratios for excess internal phosphorus per mg of algae for the five phytoplankton groups in the model was consistently greater than the 0.08% critical level proposed by Fitzgerald and Nelson (1966). This critical level was intended to approximate the operational transition between growth rate limitation by phosphorus, and phosphorus sufficiency. The model output only approached the critical level during May and August, corresponding to the two minima in average internal phosphorus level.

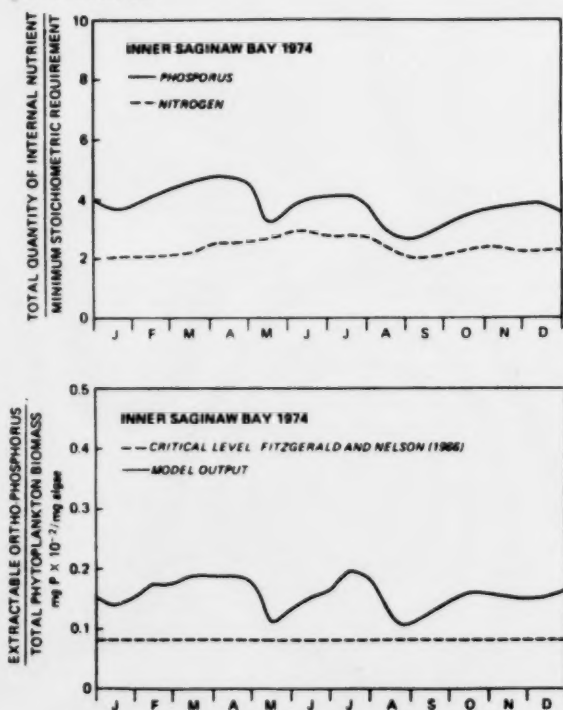


FIG. 12. Average of individual phytoplankton groups for total cellular phosphorus and nitrogen levels and excess internal (extractable) phosphorus concentrations.

The conclusion regarding nitrogen limitation was based on the assumption that the Droop equation used in the model for relating specific growth rate to internal nutrient levels was equally valid for nitrogen, as well as phosphorus. This assumption appears to be consistent with most of the evidence in the literature (Rhee 1980). Exceptions have been reported, however, in which nitrogen limited growth did not appear to follow the Droop equation (Laws and Bannister 1980, Laws and Caperton 1976).

Although nitrogen appeared to be more rate limiting than phosphorus in an average sense, important differences occurred among the individual phytoplankton groups. Figure 13 contains results for degree of saturation of the individual nutrient reduction terms in the model for diatoms, greens, and blue-greens. Results for diatoms indicated that nitrogen was rate limiting for most of the year; however, all three nutrients were equally limiting in mid-May, and extreme silicon limitation occurred from mid-May to the end of June. These results implied that, while nitrogen limited the rate of growth of diatoms for most of the year, a shift to silicon limitation was more important in determining the size of the spring diatom peak. Results for greens indicated that nitrogen was relatively more rate limiting than phosphorus for the entire year.

Results for the blue-greens were especially interesting because of dynamic changes that occurred during the period of minimum dissolved available phosphorus and nitrogen concentrations in the water column. Nitrogen limited the rate of growth of non- N_2 -fixing blue-greens for the entire year; however, the degree of phosphorus limitation nearly converged with the degree of nitrogen limitation in mid-August. For the N_2 -fixing blue-greens, nitrogen limited the rate of growth for most of the year, with the exception of a 2-month period of phosphorus limitation from mid-August to mid-October. This period coincided with the period of lowest dissolved available nitrogen concentration in the water column (see Figure 9).

The above results were a consequence of the atmospheric nitrogen fixation mechanism in the model. In response to minimal levels of dissolved available nitrogen in the water column, the N_2 -fixing blue-greens accumulated excess internal nitrogen stores, thus causing a shift from nitrogen to phosphorus growth rate limitation. In contrast, the non- N_2 -fixing blue-greens showed a substantial increase in the degree of nitrogen limitation during

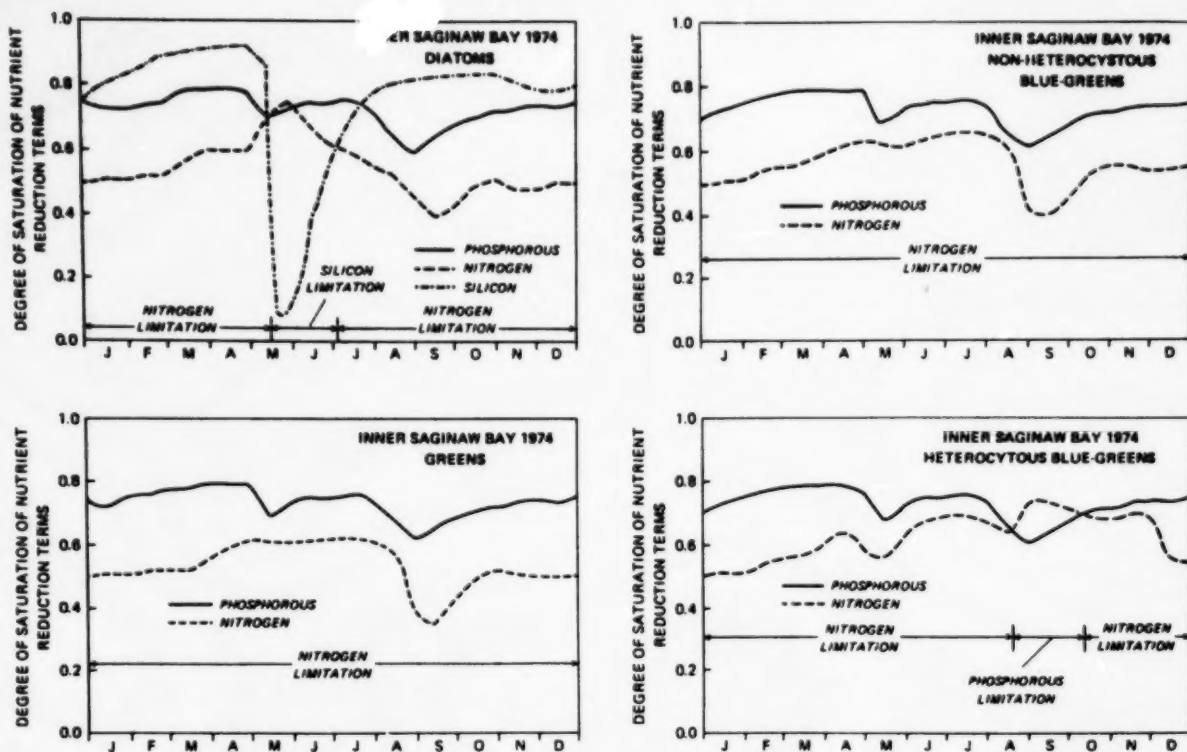


FIG. 13. Degree of saturation of individual nutrient reduction terms for the principal phytoplankton groups.

this same period. As stated above (see Figure 7), mid-August was the time when peak biomass concentrations occurred for both of the blue-green phytoplankton groups. The model output was consistent with the hypothesis that, at this time, non- N_2 -fixing blue-greens were limited by nitrogen, and N_2 -fixing blue-greens were limited by phosphorus. This set of circumstances was identical to that reported by Fitzgerald (1969) for Lake Mendota on the basis of experimental measurements of internal phosphorus and nitrogen concen-

trations in mixed blue-green blooms during the period of minimum dissolved available nutrient concentrations.

A summary of the relative importance of growth limiting factors at the times of peak phytoplankton crops is contained in Table 4. In contrast to the greater relative importance of temperature and light limitation on an annual average basis, nutrient limitation was relatively more important at the times of peak crops for each phytoplankton group. This was because peak crops tended to occur at or

TABLE 4. Relative importance of growth rate limiting factors at times of peak crops in model calibration results.

Degree of Importance	Diatoms		Phytoplankton Group			
	spring peak	fall peak	Greens	Others	Blue-Greens (non- N_2 -fixing)	Blue-greens (N_2 -fixing)
Most Important	Silicon	Nitrogen	Nitrogen	Nitrogen	Nitrogen	Transition point from nitrogen to phosphorus
	Light	Phosphorus	Light	Phosphorus	Phosphorus	
	Phosphorus and nitrogen equally	Silicon	Phosphorus	Light	Light	Light
Least Important	Temperature	Temperature	Temperature	Temperature	Temperature	Temperature

near optimal temperatures, and under conditions of nutrient depletion caused by sustained periods of comparatively fast growth.

Nutrient Recycle

The importance of internal nutrient pool kinetic mechanisms in phytoplankton models is a matter of some debate. A common argument against the use of internal nutrient pools is that they describe processes which occur over very short time scales, compared to the monthly or seasonal time scales usually of interest. A corollary to this argument is that variations of internal nutrient levels over seasonal time scales are usually small, and that the effects of such variations can either be incorporated into other state variables, or compensation made by adjusting the model coefficients. Indeed, the seasonal variations in internal nutrient levels at the present spatial scale were not large; however, arguments based on relative time scales are not the sole criterion for using internal nutrient pool kinetics. Consideration of nutrient recycle kinetics is an often-overlooked, yet extremely important, criterion for choosing between fixed and variable stoichiometry models. The choice of a phytoplankton growth kinetic mechanism includes an implicit choice of a mechanism for nutrient recycle.

To emphasize the importance of two-component nutrient recycle, sensitivity analyses were conducted in which the recycle components corresponding to excess internal nutrients for grazing, decomposition, and respiration were routed directly to the unavailable nutrient compartments in the water column instead of to the available nutrient compartments. This was not as drastic as simply "turning off" these direct recycle components because conservation of mass was still preserved. Instead, all recycled phosphorus and nitrogen were required to be shunted through the transformation process from unavailable forms to available forms before they could be reused for phytoplankton growth. This is the conventional approach to nutrient recycle used in most Monod/Michaelis-Menten, fixed stoichiometry models.

Results of the recycle sensitivity analyses are shown in Figure 14 for nutrients. For both phosphorus and nitrogen, dissolved available concentrations were substantially reduced after the spring diatom peak, relative to the calibration results. This was because most of the external loading occurred in the first half of the year, and hence, recycle processes were relatively more important later in the year.

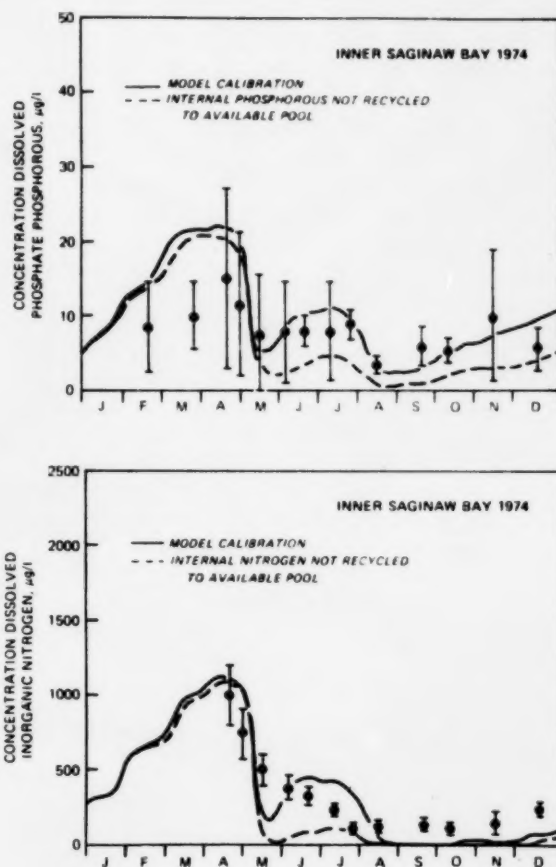


FIG. 14. Results of sensitivity analyses for dissolved available phosphorus and nitrogen when excess internal nutrients were not recycled to available pools.

Results of the recycle sensitivity analyses for phytoplankton (Table 5) are presented in terms of changes in annual integrated gross production, relative to the final calibration. This quantity was a good indicator of the relative amounts of phytoplankton produced in each functional group. In general, non-diatoms were affected to a much greater degree than diatoms. For the case where internal phosphorus was not recycled, both blue-green groups were reduced. The N_2 -fixing blue-greens were reduced by a greater degree than non- N_2 -fixing blue-greens because they were already phosphorus limited in the calibration. The non- N_2 -fixing blue-greens were relatively more nitrogen limited than phosphorus limited, and first needed to be forced into phosphorus limitation before a production decrease occurred. Consistent with this

TABLE 5. Results of model sensitivity analyses for internal phosphorus and nitrogen recycle.

Condition	Percent change in annual integrated gross production ¹				
	Diatoms	Greens	Others	Blue-greens (non-N ₂ -fixing)	Blue-greens (N ₂ -fixing)
Internal P not recycled to available pool	+6	-19	-27	-29	-39
Internal N not recycled to available pool	-2	-60	-44	-65	+60

¹Time integral of daily gross biomass production over the annual cycle.

interpretation, the non-N₂-fixing blue-greens were reduced by a greater amount when internal nitrogen was not recycled. The N₂-fixing blue-greens, however, were substantially increased when internal nitrogen was not recycled because nitrogen limitation caused reductions in all of the other phytoplankton groups and, as a result, phosphorus that was previously used by these groups was now left over for the N₂-fixing blue-greens.

An important implication of the nutrient recycle sensitivity results is that in a system which is relatively more limited by nitrogen than by phosphorus, control of nitrogen in the absence of phosphorus control could actually increase the production of N₂-fixing blue-green phytoplankton. This conclusion is consistent with results of recent experimental observations at the whole system level. Barica, Kling, and Gibson (1980) found that additions of nitrogen to a eutrophic pond appeared to stimulate non-N₂-fixing phytoplankton, including blue-greens, and to suppress N₂-fixing blue-greens. Flett *et al.* (1980) found that N₂ fixation by phytoplankton tended to occur in artificially fertilized eutrophic lakes whenever the ratio (by weight) of total phosphorus to total nitrogen in the input loadings was less than approximately 10. For the Saginaw River, this ratio was approximately 11 (Table 1). The present results suggest that Saginaw Bay would have been near the threshold for accelerated production of N₂-fixing blue-greens, had there been a reduction in nitrogen loading.

Relative Contribution of Phosphorus Sources

The above results implied that while nitrogen and silicon were important in the phytoplankton-nutrient dynamics in Saginaw Bay, the supply of phosphorus would ultimately determine the size of the blue-green component of the total crop because N₂-fixing blue-greens do not have absolute require-

ments for dissolved nitrogen and silicon. Because of this, it is pertinent to investigate the relative importance of the various possible sources of available phosphorus in the water column.

Figure 15 contains results of a process analysis of the sources of phosphorus available to the phytoplankton. Phytoplankton net phosphorus uptake rate over the annual cycle has been juxtaposed against the relative contributions of various

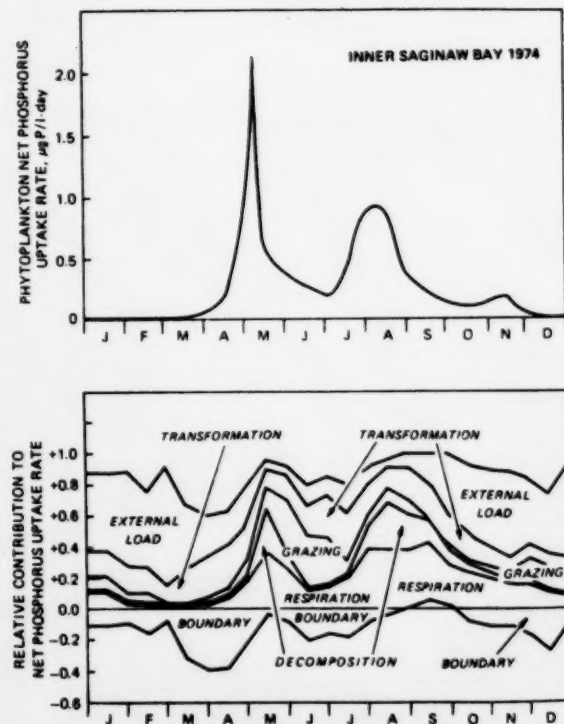


FIG. 15. Results of process level analyses of phytoplankton-phosphorus dynamics.

processes responsible for supplying dissolved available phosphorus to the water column. At any given time, it can be determined which processes were contributing more significantly to the phosphorus requirements of the phytoplankton. The sum of absolute values of the relative contributions was equal to unity. All processes except boundary flow constituted gains relative to phytoplankton uptake and were assigned positive values. Boundary flow could constitute either a gain or a loss relative to phytoplankton uptake and was assigned either a positive or a negative value, respectively.

One of the most noteworthy aspects of the phytoplankton-phosphorus dynamics was that phosphorus requirements of spring and fall diatom crops were satisfied primarily by external loading, and phosphorus requirements of summer blue-green crops were satisfied primarily by recycle processes within the water column. This was consistent with results of the nutrient recycle sensitivity analyses. During the July-September period, external phosphorus load was at a minimum, and there was an almost continual loss of dissolved available phosphorus from the inner bay due to boundary flow. Recycle from zooplankton grazing, and subsequent excretion, contributed up to 35 percent of the available phosphorus required for phytoplankton uptake after the spring diatom peak. Recycle from decomposition and respiration together contributed approximately 70 percent of the available phosphorus for blue-greens during their peak requirement in August.

Transformation refers to the conversion process from unavailable phosphorus to available phosphorus. The relative contribution of transformation to net phytoplankton uptake ranged from 10 to 25 percent over the annual cycle. In spring, the transformation contribution was determined primarily by the large concentration of phosphorus in the water column due to high external loading. In summer, this contribution was determined primarily by the elevated temperature.

Sensitivity Analyses

Another way to use a calibrated simulation model as a tool to gain insight into system dynamics is to conduct sensitivity analyses by varying model coefficients and/or forcing functions. An extensive series of such analyses were conducted with the present model. Results were expressed in terms of percent changes in annual integrated gross productions, relative to the final calibration. Table 6 contains summary results for average phytoplank-

TABLE 6. Summary of average responses to sensitivity analyses.

Parameter Varied	Average Absolute Percent Change for all Phytoplankton Groups in Response to ± 50 Percent Variation
XTINCO	180
RAMAX	145
RZMAX	104
ZASSIM	86
RRESP	82
T	78
KZSAT	42
P-Uptake Half-Saturation Concentration	29
PDETH	28
SSA	22 (53 for diatoms)
Q	17
RINM	16
RLYS	14
TOPSNK, TONSNK, TOSSNK	14
BDETH	14
AZMIN	11
RADSAT	8
N-Uptake Half-Saturation Concentration	8
KSCM	8
ASINK	6
RADINC	6
RTOP, RTON, RTOS	5
RIPM	0

ton responses to each parameter varied, in order of decreasing sensitivity.

In interpreting the results, it is important to maintain a proper perspective. The following considerations are pertinent:

1. Responses were not always symmetrical about the calibration results for equal plus and minus variations in a given parameter.
2. Some individual phytoplankton groups responded to greater degrees than other groups to variations in certain parameters.
3. Some of the parameter variations only had direct effects on certain phytoplankton groups. For example, variations in silicon-related parameters only had direct effects on the diatoms.

Mindful of these qualifications, the results can be a useful guide to the relative importance of the various mechanisms and coefficients in the model.

One of the most significant results was the extreme sensitivity of the phytoplankton to varia-

tions in the underwater light environment (XTINCO), and the relative insensitivity to variations in incident solar radiation (RADINC). Phytoplankton responses were relatively sensitive to temperature variations, but only moderately sensitive to variations in hydraulic detention time (Q). This latter result implied that the dynamic behavior of the calibration results was primarily a reflection of the biological-chemical kinetics in the model, and not of the boundary conditions.

In general, the phytoplankton were sensitive to variations in maximum growth and ingestion rates for the phytoplankton and zooplankton, respectively, and to variations in the associated half-saturation concentrations. The phytoplankton were more sensitive to variations in zooplankton assimilation efficiency (ZASSIM) and phytoplankton respiration rate (RRESP) than to variations in any other loss-related parameter. Consistent with the previous discussion on limiting nutrients, the diatoms were especially sensitive to variations in SSA, percent silica by dry weight. The value for this coefficient had a strong influence on the size of the spring diatom peak.

The phytoplankton were relatively insensitive to variations in net sinking rates for phytoplankton (ASINK) and unavailable nutrient forms (TOPSNK, TONSNK, TOSSNK). This was probably due to the relatively short hydraulic detention time of the bay. In addition, the values found for these coefficients in the calibration were apparently consistent with a relatively high degree of vertical dispersion in the water column.

It was significant to note that the phytoplankton were relatively insensitive to variations in conversion rates from unavailable to available nutrient forms (RTOP, RTON, RTOS). This was most probably due to the relatively short hydraulic detention time of the bay. This result was the opposite of what would be expected for systems with much longer hydraulic detention times, such as the other major basins in the Great Lakes.

CONCLUSIONS

It was demonstrated that information on the properties and dynamics of phytoplankton, zooplankton, and nutrients could be synthesized within a mass balance modeling framework. This framework successfully described the major patterns of phytoplankton growth and seasonal succession observed in eutrophic environments. Although this study included only the Saginaw Bay system,

results of process level analyses with the calibrated model provided many insights which are applicable to lakes in general.

The concept of a single limiting factor for phytoplankton growth was found to be overly simplistic. An important distinction should be made between factors controlling phytoplankton growth on an annual average basis, and factors controlling sizes of peak phytoplankton crops. Temperature and light were relatively more important controlling factors than nutrients on an annual average basis; however, as a consequence of nutrient depletion, nutrients became relatively more important during periods of peak phytoplankton crops. Another important distinction that should be made is that between factors controlling the phytoplankton crop in an average sense, and factors controlling the individual functional groups. At various times, and for various phytoplankton groups, more than one nutrient was important in controlling rate of growth and/or peak concentration. Furthermore, the nutrient which may control peak phytoplankton crop may not always be the same nutrient which controls growth rate over seasonal, or annual time scales.

An important implication of the above results is that if bioassays are used for determining nutrient limitation in a given system, then the results may depend on the timing and proportions of the various individual phytoplankton groups. If such results are to be used for developing a nutrient control strategy, then careful interpretation is required, consistent with the objectives of the strategy.

The soundness of pursuing a strategy of phosphorus control on Saginaw Bay was confirmed. Water quality issues on the bay were related to excessive production of blue-green phytoplankton. Because of the potential for nitrogen fixation, nitrogen control in the absence of phosphorus control could have caused an increase in the production of N_2 -fixing blue-greens.

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ABBREVIATIONS AND SYMBOLS

A	—phytoplankton concentration in mg dry wt/L
ADUM _{kI}	—minimum concentration of phytoplankton I necessary for zooplankton k to begin grazing
ASINK	—phytoplankton sinking rate in meters/day
AZMIN _k	—refuge concentration of phytoplankton below which zooplankton k can not graze
BDETH	—maximum zooplankton death rate in day ⁻¹
CONCP	—internal concentration factors for phos-

CONCN	phorus and nitrogen, respectively (dimensionless)		(grazed) by zooplankton in mg A/liter day
FACT	—phytoplankton cell size in mg dry wt/cell	RAMAX	—phytoplankton maximum growth rate at 20°C in day ⁻¹
f(L)	—phytoplankton light reduction factor (dimensionless)	RLYS	—phytoplankton decomposition rate in liter/mg day
f(T)	—phytoplankton temperature reduction factor (dimensionless)	RRESP	—phytoplankton respiration rate in day ⁻¹
Kc	—light extinction coefficient in meter ⁻¹	RTOP,	—rates of transformation from available
KNCELL	—intracellular half-saturation constant for nitrogen-dependent growth in moles N/cell	RTON,	nutrient forms (phosphorus, nitrogen, silicon) to available forms in day ⁻¹
KPCCELL	—intracellular half-saturation constant for phosphorus-dependent growth in moles P/cell	RTOS	
KSCM	—half-saturation constant for silicon-dependent growth of diatoms in moles Si/L	RZ	—zooplankton specific growth rate in day ⁻¹
KZSAT _k	—half-saturation concentration of phytoplankton for grazing by zooplankton <i>k</i>	RZMAX	—zooplankton maximum ingestion rate in day ⁻¹
P, N	—actual moles of phosphorus (nitrogen) per phytoplankton cell	RZPEX,	—nutrient (phosphorus, nitrogen, silicon) excretion by zooplankton to unavailable nutrient pool in moles/mg zooplankton-day
PCA, NCA	—intracellular available phosphorus (nitrogen) concentrations in moles/liter cell volume	RZNEX,	
PCAMIN,	—minimum intracellular concentrations, corresponding to PSAMIN and NSAMIN, respectively, for available phosphorus (nitrogen) in moles/liter cell volume	RZSEX	
NCAMIN		SPGR	—phytoplankton specific growth rate in day ⁻¹
PCM,	—concentrations of available nutrients (phosphorus, nitrogen, silicon) in water column in moles/L	SSA	—silicon composition of diatoms in moles/mg dry wt
NCM,		T	—temperature in °C
SCM		TCROP	—total phytoplankton concentration in mg dry wt/L
PDETH	—maximum predatory death rate for zooplankton in liter/mg-day	TOP, TON,	—concentration of unavailable nutrients (phosphorus, nitrogen, silicon) in moles/L
PHOTO	—photoperiod (dimensionless)	TOS	
PK1, NK1	—affinity coefficient for phosphorus (nitrogen) uptake mechanism in liter/mole	TOPSNK,	—sinking rates of unavailable nutrient forms (phosphorus, nitrogen, silicon) in meters/day
PO, NO	—minimum cell quota of phosphorus (nitrogen) per phytoplankton cell in moles/cell	TONSNK	
PSA, NSA	—actual total phosphorus (nitrogen) in phytoplankton cells in moles/mg dry wt	TOSSNK	
PSAMIN,	—minimum quota of phosphorus (nitrogen) in phytoplankton cells in moles/mg dry wt	V	—inner bay volume in liters
NSAMIN		WPCM,	—external loading rates of available nutrients (phosphorus, nitrogen, silicon) in moles/day
PSAT _k	—saturation concentration of zooplankton <i>k</i> above which predatory death rate remains constant	WNCM,	
Q	—water circulation rate in volume/day	WSCM	
RIPM,	—maximum phosphorus (nitrogen) uptake rate in day ⁻¹	WTOP,	—external loading rates of unavailable nutrients (phosphorus, nitrogen, silicon) in moles/day
RINM		WTON,	
RADINC	—incident solar radiation in langley/day	WTOS	
RADSAT	—saturation light intensity for phytoplankton growth in langley/day	Z	—zooplankton concentration in mg dry wt/L
RAGRZD _i	—rate at which phytoplankton <i>i</i> is ingested	ZASSIM	—zooplankton assimilation efficiency (dimensionless)
		ZEFF _{kl}	—ingestion efficiency of zooplankton <i>k</i> for phytoplankton <i>l</i> (dimensionless)
		ZDETH	—specific zooplankton death rate in day ⁻¹
		ZKDUM	—effective half-saturation concentration of total phytoplankton for grazing by zooplankton
		ZSAFE	—refuge concentration of zooplankton below which predatory grazing does not occur

Note: The addition of the suffix "BD" to a variable refers to the boundary value of the variable.

APPENDIX A. Model equations.

STATE VARIABLE EQUATIONS

For each phytoplankton type, i , the rate of change of intracellular phosphorus is given by:

$$1.0 \quad \frac{d(A_i PSA_i)}{dt} = \text{boundary contribution} + \text{net uptake} - \text{grazing} - \text{decomposition} - \text{respiration} - \text{sinking}$$

$$1.1 \quad \text{boundary contribution} = \frac{Q}{V} (ABD_i PSA_{BD_i} - A_i PSA_i)$$

$$1.2 \quad \text{net uptake} = A_i R1PM_i f(T)_i f(L)_i \times (0.322 \times 10^{-4}) \frac{\text{moles P}}{\text{mg P}} \left[\frac{1}{1 + PK1_i PCA_i} - \frac{1}{1 + PK1_i PCM} \right]$$

$$1.3 \quad \text{grazing} = PSA_i RAGRZD_i$$

$$1.4 \quad \text{decomposition} = A_i PSA_i RLYS_i TCROP \cdot 1.08^{(T-20)}$$

$$1.5 \quad \text{respiration} = A_i PSA_i RRESP_i f(T)_i$$

$$1.6 \quad \text{sinking} = A_i PSA_i ASINK_i / \text{DEPTH}$$

Expanding by the chain rule for derivatives:

$$2.0 \quad \frac{d(A_i PSA_i)}{dt} = A_i \frac{dPSA_i}{dt} + PSA_i \frac{dA_i}{dt}$$

For each phytoplankton type, i , the rate of change in biomass is given by:

$$3.0 \quad \frac{dA_i}{dt} = \text{boundary contribution} + \text{gross production} - \text{grazing} - \text{decomposition} - \text{respiration} - \text{sinking}$$

$$3.1 \quad \text{boundary contribution} = \frac{Q}{V} (ABD_i - A_i)$$

$$3.2 \quad \text{gross production} = A_i SPGR_i$$

Specific growth rate of phytoplankton i , $SPGR_i$, is set equal to the minimum value of the following functions:

$$3.2.1 \quad RAMAX_i f(T)_i f(L)_i [(P-PO)/(KPCELL + (P-PO))]$$

$$3.2.2 \quad RAMAX_i f(T)_i f(L)_i [(N-NO)/(KNCELL + (N-NO))]$$

$$3.2.3 \quad RAMAX_i f(T)_i f(L)_i [SCM/(KSCM + SCM)]$$

$$3.3 \quad \text{grazing} = RAGRZD_i$$

$$3.4 \quad \text{decomposition} = A_i RLYS_i TCROP \cdot 1.08^{(T-20)}$$

$$3.5 \quad \text{respiration} = A_i RRESP_i 1.08^{(T-20)}$$

APPENDIX A, continued.

$$3.6 \quad \text{sinking} = A_i \text{ASINK}_i / \text{DEPTH}$$

In equation 3.0, it is assumed that the contribution to the derivative due to changes in intracellular phosphorus is negligible.

Setting the right hand sides of equations 1.0 and 2.0 equal and substituting equation 3.0 gives the following equation for the state variable PSA_i :

$$4.0 \quad \frac{d\text{PSA}_i}{dt} = \text{boundary contribution} + \text{net uptake} - \text{gross production}$$

$$4.1 \quad \text{boundary contribution} = \frac{Q}{V} \text{ABD}_i (\text{PSABD}_i - \text{PSA}_i) / A_i$$

$$4.2 \quad \text{net uptake} = R1\text{PM}_i f(T)_i f(L)_i (0.322 \times 10^{-4}) \frac{\text{moles P}}{\text{mg P}} \times \left| \frac{1}{1 + \text{PK1}_i \text{PCA}_i} - \frac{1}{1 + \text{PK1}_i \text{PCM}} \right|$$

$$4.3 \quad \text{gross production} = \text{PSA}_i \text{SPGR}_i$$

$$5.0 \quad \frac{d\text{PCM}}{dt} = \text{boundary contribution} - \text{net uptake} + \text{respiration} + \text{zooplankton excretion} + \text{decomposition} \\ + \text{transformation} + \text{external loading}$$

$$5.1 \quad \text{boundary contribution} = \frac{Q}{V} (\text{PCMBD} - \text{PCM})$$

$$5.2 \quad \text{net uptake} = (0.322 \times 10^{-4}) \frac{\text{moles P}}{\text{mg P}} \\ \times \sum_i A_i R1\text{PM}_i f(T)_i f(L)_i \left| \frac{1}{1 + \text{PK1}_i \text{PCA}_i} - \frac{1}{1 + \text{PK1}_i \text{PCM}} \right|$$

$$5.3 \quad \text{respiration} = \sum_i A_i (\text{PSA}_i - \text{PSAMIN}_i) \text{RRESP}_i 1.08^{(T-20)}$$

$$5.4 \quad \text{zooplankton excretion} = \sum_i (\text{PSA}_i - \text{PSAMIN}_i) \text{RAGRZD}_i$$

$$5.5 \quad \text{decomposition} = \text{TCROP} \cdot 1.08^{(T-20)} \sum_i A_i (\text{PSA}_i - \text{PSAMIN}_i) \text{RLYS}_i$$

$$5.6 \quad \text{transformation} = \text{RTOP} \cdot \text{TOP} \cdot 1.08^{(T-20)}$$

$$5.7 \quad \text{external loading} = \text{WPCM} / V$$

The equation for nitrogen concentration, NCM , is functionally identical to equation 5.0 for phosphorus concentration.

$$6.0 \quad \frac{d\text{SCM}}{dt} = \text{boundary contribution} - \text{gross diatom production} + \text{transformation} + \text{external loading}$$

APPENDIX A, continued.

- 6.1 boundary contribution = $\frac{Q}{V}$ (SCMBD-SCM)
- 6.2 gross diatom production = $\sum_{\text{diatoms}} A_i \text{SSA}_i \text{SPGR}_i$
- 6.3 transformation = $\text{RTOS} \cdot \text{TOS} \cdot 1.08^{(T-20)}$
- 6.4 external loading = WSCM/V
- 7.0 $\frac{dZ_k}{dt}$ = boundary contribution + growth rate - death rate
- 7.1 boundary contribution = $\frac{Q}{V}$ ($\text{ZBD}_k - Z_k$)
- 7.2 growth rate = $\text{RZ}_k Z_k$ (refer to 10.0)
- 7.3 death rate = $\text{ZDETH}_k Z_k$ (refer to 14.1 and 14.2)
- 8.0 $\frac{d\text{TOP}}{dt}$ = boundary contribution + respiration + decomposition + zooplankton excretion + zooplankton death
- transformation - sinking + external loading
- 8.1 boundary contribution = $\frac{Q}{V}$ ($\text{TOPBD} - \text{TOP}$)
- 8.2 respiration = $\sum_i A_i \text{PSAMIN}_i \text{RRESP}_i 1.08^{(T-20)}$
- 8.3 decomposition = $\sum_i A_i \text{PSAMIN}_i \text{RLYS}_i \text{TCROP} \cdot 1.08^{(T-20)}$
- 8.4 zooplankton excretion = $\sum_k \text{RZPEX}_k Z_k$ (refer to 12.0)
- 8.5 zooplankton death = $\sum_k \text{BDETH}_k Z_k (0.161 \times 10^{-7}) \frac{\text{mole P}}{\text{mg Z}} 1.08^{(T-20)}$
- 8.6 transformation = $\text{RTOP} \cdot \text{TOP} \cdot 1.08^{(T-20)}$
- 8.7 sinking = $\text{TOP} \cdot \text{TOPSNK}/\text{DEPTH}$
- 8.8 external loading = WTOP/V

The equation for unavailable nitrogen, TON, is functionally identical to equation 8.0 for unavailable phosphorus.

- 9.0 $\frac{d\text{TOS}}{dt}$ = boundary contribution + respiration + decomposition + zooplankton excretion - transformation
- sinking + external loading
- 9.1 boundary contribution = $\frac{Q}{V}$ ($\text{TOSBD} - \text{TOS}$)

APPENDIX A, continued.

- 9.2 respiration = $\sum_{\text{diatoms}} A_i \text{SSA}_i \text{RRESP}_i 1.08^{(T-20)}$
- 9.3 decomposition = $\sum_{\text{diatoms}} A_i \text{SSA}_i \text{RLYS}_i \text{TCROP}_i 1.08^{(T-20)}$
- 9.4 zooplankton excretion = $\sum_{\text{diatoms}} \text{RAGRZD}_i \text{SSA}_i$ (refer to 11.0)
- 9.5 transformation = $\text{RTOS} \cdot \text{TOS} \cdot 1.08^{(T-20)}$
- 9.6 sinking = $\text{TOS} \cdot \text{TOSSNK} / \text{DEPTH}$
- 9.7 external loading = $\text{WTOS} / \text{DEVH}$

PROCESS RATE EQUATIONS

Specific growth rate for zooplankton k :

$$10.0 \quad \text{RZ}_k = \text{RZMAX}_k \text{ZASSIM}_k 1.08^{(T-20)} \left[\frac{\sum_l \text{ZEFF}_{kl} A_l - \text{AZMIN}_k}{\text{ZKDUM}_k + \sum_l \text{ZEFF}_{kl} A_l - \text{AZMIN}_k} \right]$$

$$10.1 \quad \text{ZKDUM}_k = \left[\frac{\sum_l \text{ZEFF}_{kl} A_l - \text{AZMIN}_k}{\sum_l \text{ZEFF}_{kl} A_l} \right] \text{KZSAT}_k$$

Rate at which phytoplankton l is grazed by zooplankton:

$$11.0 \quad \text{RAGRZD}_l = 1.08^{(T-20)} \sum_k \left[\frac{\text{RZMAX}_k \text{Z}_k (\text{ZEFF}_{kl} A_l - \text{ADUM}_{kl})}{\text{ZKDUM}_k + \sum_l \text{ZEFF}_{kl} A_l - \text{AZMIN}_k} \right]$$

$$11.1 \quad \text{ADUM}_{kl} = \frac{\text{ZEFF}_{kl} A_l}{\sum_l \text{ZEFF}_{kl} A_l} \text{AZMIN}_k$$

Note: $\sum_l \text{ADUM}_{kl} = \text{AZMIN}_k$

Rate at which phosphorus is excreted to the unavailable pool by zooplankton k :

$$12.0 \quad \text{RZPEX}_k = (1 - \text{ZASSIM}_k) \text{RZMAX}_k 1.08^{(T-20)} \left[\frac{\sum_l (\text{ZEFF}_{kl} A_l - \text{ADUM}_{kl}) \text{PSAMIN}_l}{\text{ZKDUM}_k + \sum_l \text{ZEFF}_{kl} A_l - \text{AZMIN}_k} \right]$$

The process rate equation for nitrogen excretion is functionally identical to equation 12.0 for phosphorus.

Rate at which silicon is excreted to the unavailable pool by zooplankton k :

APPENDIX A, continued.

$$13.0 \quad RZSEX_k = RZMAX_k 1.08^{(T-20)} \left[\frac{\sum_{\text{diatoms}} (ZEFF_{kl} A_l - ADUM_{kl}) SSA_l}{ZKDUM_k + \sum_l ZEFF_{kl} A_l - AZMIN_k} \right]$$

Zooplankton death rate is given by:

$$14.1 \quad ZDETH_k = BDETH_k 1.08^{(T-20)} \quad Z_k < ZSAFE_k$$

$$14.2 \quad ZDETH_k = (BDETH_k + PDETH_k Z_k) 1.08^{(T-20)} \quad PSAT_k > Z_k > ZSAFE_k$$

MISCELLANEOUS FUNCTIONS

$$15.0 \quad PSAMIN_l = PO_l / FACT_l$$

$$15.1 \quad PCAMIN_l = PSAMIN_l (0.25 \times 10^6) / CONCP_l$$

$$15.2 \quad f(L) = \frac{(2.718) PHOTO}{K_e \cdot DEPTH} \left| e^{-\alpha_1} - e^{-\alpha_0} \right|$$

$$15.2.1 \quad PHOTO = 0.64 \{ 0.78 - 0.22 [\text{SINE}(6.28 \cdot (\text{TIME} + 90) / 365)] \}$$

$$15.2.2 \quad \alpha_0 = \text{RADINC} / \text{RADSAT}_l$$

$$15.2.3 \quad \alpha_1 = \alpha_0 e^{-K_e \cdot DEPTH}$$

$$15.2.4 \quad K_e = 1.195 / \text{Secchi Depth} + 0.159$$

RADINC, Secchi Depth and T were specified externally on a daily basis using linear interpolation between measured values.

PHYTOPLANKTON TEMPERATURE REDUCTION FACTORS

$$16.0 \quad f(T)_{\text{diatoms}} = \begin{aligned} &= 0.2(T-2)/1.6 && T < 10 \\ &= 1 && 10 < T < 14 \\ &= (1.6 - 0.2(T-14))/1.6 && T > 14 \end{aligned}$$

$$16.1 \quad f(T)_{\text{greens}} = 0.0824(T-3)/1.4$$

$$16.2 \quad f(T)_{\text{others}} = 0.0706(T-3)/1.2$$

$$16.3 \quad f(T)_{\text{non-heterocystous blue-greens}} = \begin{aligned} &= 0.03125(T-3) && T < 11 \\ &= (0.25 + 0.0833(T-11)) && T > 11 \end{aligned}$$

$$16.4 \quad f(T)_{\text{heterocystous blue-greens}} = \begin{aligned} &= 0.01875(T-3)/0.7 && T < 11 \\ &= (0.15 + 0.0611(T-11))/0.7 && T > 11 \end{aligned}$$

Note: The minimum value for $f(T)$ for each species is arbitrarily specified at 0.01 day⁻¹.

APPENDIX B. Summary of phytoplankton coefficients.

Coefficients	Units	Phytoplankton Type				
		Diatoms	Greens	Others	Blue-Greens (non-N ₂)	Blue-Greens (N ₂)
RIPM	day ⁻¹	0.500	0.500	0.500	0.500	0.500
PKI	liters/ mole	0.518×10 ⁶	0.167×10 ⁷	0.518×10 ⁶	0.200×10 ⁷	0.518×10 ⁶
PO	mole P/cell	0.724×10 ⁻¹³	0.312×10 ⁻¹⁴	0.148×10 ⁻¹³	0.566×10 ⁻¹⁴	0.488×10 ⁻¹⁴
CONCP	—	0.250×10 ⁶	0.250×10 ⁶	0.250×10 ⁶	0.356×10 ⁶	0.356×10 ⁶
KPCCELL	mole P/cell	0.724×10 ⁻¹³	0.312×10 ⁻¹⁴	0.148×10 ⁻¹³	0.566×10 ⁻¹⁴	0.488×10 ⁻¹⁴
RINM	day ⁻¹	0.125	0.125	0.125	0.125	0.125
NKI	liters/ mole	0.100×10 ⁷	0.100×10 ⁷	0.100×10 ⁷	0.100×10 ⁷	0.100×10 ⁷
NO	mole N/cell	0.801×10 ⁻¹¹	0.345×10 ⁻¹²	0.163×10 ⁻¹¹	0.438×10 ⁻¹²	0.377×10 ⁻¹²
CONCN	—	0.208×10 ⁷	0.208×10 ⁷	0.208×10 ⁷	0.208×10 ⁷	0.208×10 ⁷
KNCCELL	mole N/cell	0.801×10 ⁻¹¹	0.345×10 ⁻¹²	0.163×10 ⁻¹¹	0.438×10 ⁻¹²	0.377×10 ⁻¹²
SSA	mole Si/ mg	0.334×10 ⁻⁵	—	—	—	—
KSCM	mole Si/ liter	0.357×10 ⁻⁵	—	—	—	—
RAMAX	day ⁻¹	1.6	1.4	1.2	1.0	0.70
ASINK	meter/ day	0.05	0.05	0.05	0.05	0.05
RLYS	liters/ mg day	0.004	0.004	0.004	0.012	0.012
FACT	mg/ cell	0.450×10 ⁻⁵	0.194×10 ⁻⁶	0.918×10 ⁻⁶	0.246×10 ⁻⁶	0.212×10 ⁻⁶
RADSAT	langleys/ day	100	100	100	50	50
RRESP	day ⁻¹	0.05	0.05	0.05	0.05	0.05

APPENDIX C. Summary of zooplankton coefficients.

Coefficient	Unit	Zooplankton Type	
		Fast Ingestor	Slow Ingestor
RZMAX	day ⁻¹	0.70	0.10
ZASSIM	—	0.60	0.60
KZSAT	mg/ liter	1.0	1.0
AZMIN	mg/ liter	0.20	0.20
BDETH	day ⁻¹	0.05	0.01
PDETH	day ⁻¹	0.50	0.10
ZSAFE	mg/ liter	0.01	0.01
PSAT	mg/ liter	1.0	1.0

APPENDIX D. Summary of coefficients for unavailable nutrients.

Coefficient	Units	Value
RTOP, RTON, RTOS	day ⁻¹	0.005
TOPSNK, TONSNK, TOSSNK	meters/ day	0.05